Insects in forests

Assemblages, effects of tree diversity and population dynamics

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Marburg, den 30.07.2014 Urwa Alalouni

Contents

Chapter 1

Chapter 2

Chapter 3

Chapter 4

Chapter 1

General introduction

General introduction

Insects play an essential role in forest ecosystems, e.g., by affecting the primary production and evolution of plants. They are also a critical link between plants and higher trophic levels (Mattson 1980; Crawley 1989; 1997). Forests with their vertical stratifications (e.g., canopy and understorey) support a high diversity of insects (Gunnarsson 1990; Baines et al. 1994; Humphrey et al. 1999). This includes a high diversity of insect guilds as well as the diversity within guilds (Dajoz 2000). The relationship between insects and forests is controlled by tree-insect interactions (Lieutier 2006). In turn, tree-insect interactions are influenced by biotic (e.g., tree diversity and natural enemies) and abiotic factors, e.g., temperature and carbon dioxide (Larsson 1989; Herms & Mattson 1992; Koricheva et al. 1998). Phytophagous insects are a part of a diverse group of forest insects. On the one hand, these insects feed on leaves and can at high densities cause severe defoliation and damage to forests (Williams et al. 1991; Lovett et al. 2002). On the other hand, phytophagous insects can be beneficial to forest growth. Light defoliation assists nutrient cycling, plant population and predator-prey population dynamics (Mattson & Addy 1975; Mattson 1980). Thus, phytophagous insects play an important role in the energy flux in forest ecosystems (Mattson et al. 1975; Hammond & Miller 1998). In addition to the high ecological and economic importance, some insects such as Lepidoptera are indicator species for monitoring the conservation value of forests (Kerr et al. 1998; Brown & Freitas 2000; Kitching et al. 2000). Hence, understanding the relationship between insects and forests is a key factor for better management and conservation of insect communities and forest ecosystems.

The assemblages of insects in forests

Forests harbour an enormous diversity of organisms (Smith & Smith 2000). Understanding the patterns of such diversity requires exploring the processes that control the distribution and assemblages of species (Drake 1990; Cottenie 2005). Such processes are usually influenced by spatial scale, habitat type, local environment, organism size and dispersal ability (Leibold 1998; Hillebrand 2004; Soininen 2010).

The decrease in the similarity of species compositions with the increase in spatial distance is considered one of the most important patterns describing the diversity of species across geographical settings (Tobler 1970; Nekola & White 1999; Morlon et al. 2008; Thieltges et al. 2009). Three different processes have been proposed to explain these patterns: (1) environmental processes, (2) neutral processes and (3) biotic interactions such as intra-

and interspecific competition (Hubbell 2001; Pitman et al. 2001; Leibold et al. 2004; Tscharntke & Brandl 2004; Cottenie 2005).

The heterogeneity of environment across geographic regions causes variations in the composition of species assemblages, because environmental factors might work as filters for species (Hanski & Heino 2003; Müller et al. 2011). When different species have access to the same habitat or have the same dispersal ability, only species that can cope with local environment are able to persist (Leibold 1998; Chase & Leibold 2003). Hence, changes in species compositions will be observed with the change in environment across spatial distance. Yet, environmental variations are spatially autocorrelated and various environmental factors show different spatial autocorrelation patterns (Dormann et al. 2007; Tuomisto et al. 2012).

Neutral processes with the assumption that species from the same trophic level are ecologically equal can also lead to spatial autocorrelation of species compositions. According to this view, species might be abundant or rare at any area regardless of the environmental heterogeneity, and limited dispersal of species leads to spatially autocorrelated variations in compositions (Hubbell 2001). As a result, the homogeneity of species compositions decreases with increasing distances between habitat patches (Condit et al. 2002). Species mobility is important in this regard. Species with a high propensity for dispersal, especially for large distances, are more likely to move from and to new habitats and connect habitats (Bush & Whittaker 1991; Weddell 1991). However, dispersal is also dangerous for species, because it is not guaranteed that a dispersing individual will find suitable hosts (Müller et al. 2011).

The biotic interaction processes have led to speculations that good competitors should dominate assemblages, whereas species with low competitive abilities should be rare (Pitman et al. 2001; Tuomisto & Ruokolainen 2006). In this perspective, the compositions of species are expected to be relatively similar across spatial distance as long as no trade-off between competitive ability and dispersal propensity exists. Furthermore, the environmental and geographical changes have little influences on the variations in species compositions (Tuomisto & Ruokolainen 2006).

Analysing the relative role of spatial and environmental processes in species compositions provides important information for the conservation and the management of forests (Tuomisto et al. 2003). Two powerful statistical approaches were proposed for disentangling the effects of environment and spatial distance on species assemblages and distribution. The first approach deals with the variations in compositional similarity of species abundances across geographical and environmental distances (distance approach; Nekola et al. 1999). The second approach models the raw data of species (species abundances x sites

matrices) to variables measuring space and environment (raw approach; Legendre et al. 2005). However, these two approaches are controversial in terms of the ecological question they answer (Tuomisto et al. 2006; Legendre et al. 2008; Tuomisto & Ruokolainen 2008).

In the second chapter, I study the effects of environmental and neutral processes on the variations in the composition of moth assemblages across Bavarian forests. I compare the raw and distance approaches to evaluate the relative role of environmental and spatial distance on species compositions. The results underline the need for developing statistical approaches that give precise and consistent predictions for the relative importance of environmental versus spatial distance.

Tree diversity and insects

The interactions between herbivorous insects and trees have large effects on the relationship between insects and forests (Lieutier 2006). These interactions are influenced by biotic and abiotic factors (Larsson 1989; Herms & Mattson 1992; Koricheva et al. 1998). The diversity of trees is considered one of the most important factors that affect not only tree-herbivore interactions, but also the entire ecosystem, e.g., food web stability and diversity of arthropods (Haddad et al 2009, 2011). Furthermore, the occurrence and performance of herbivorous insects ultimately depend on the availability of suitable host plants. Since many insects are specialized feeders, an increase in the number of tree species should increase the number of insect species, which affect insect compositions and population dynamics. However, this is not necessarily reflected by the intensity of herbivory in higher diverse tree stands. Thus, studying the effects of tree diversity on herbivorous insects is important for understanding: (1) the outcomes of the interactions between tree diversity and herbivores, (2) mechanisms that explain the outcomes of such interactions, (3) the effects of the outcomes on other ecosystem functions, assembly structure of herbivores and population dynamics and (4) new approaches for the management of forest ecosystems.

Contrasting patterns were proposed to describe the interactions between plant diversity and herbivorous insects. On the one hand, increasing plant diversity was reported to increase the abundance of and damage by herbivores (Mulder et al. 1999; Prieur-Richard et al. 2002; Schuldt et al. 2010). On the other hand, a decrease in the abundance of and damage by herbivores was attributed to the increase in plant diversity (Scherber et al. 2006; Jactel & Brockerhoff 2007; Unsicker et al. 2008). Other studies indicated that plant diversity-herbivore interactions do not follow general and uniform patterns, but are highly variable and strongly

dependent on many factors such as host tree species, stand characteristics and the type of the herbivore (Vehvilainen et al. 2006; Kaitaniemi et al. 2007; Vehvilainen et al. 2007).

The "associational susceptibility" hypothesis was developed to account for the increase in herbivore damage with increasing plant diversity (Wada et al. 2000; White & Whitham 2000; Barbosa et al. 2009). According to this hypothesis, an increase in population size could trigger herbivores, especially generalists on preferred host plants, to switch onto other host plants. Furthermore, the diverse diet increases the performance and abundance of the herbivores which increase damage to plants (Brown & Ewel 1987; Wada et al. 2000; White et al. 2000). The concept of "Associational resistance" was introduced to explain the possible decrease of herbivore damage with increased plant diversity. According to this view, natural enemies, resource dilution and/or plant apparency drive the decrease in herbivore damage with increasing plant diversity (Tahvanainen & Root 1972; Root 1973; Barbosa et al. 2009).

The effects of tree diversity on the interaction between herbivorous insects and their hosts are rarely investigated for several compositions of tree stands in experimental studies (Baeten et al. 2013). In the third chapter, I investigate the effects of tree diversity on insect herbivory and the performance of a generalist herbivore in field and lab experiments. Specifically, I investigate: (1) whether the effects of tree diversity will lead to a decrease or increase in the herbivore damage in the field, (2) whether such effects are caused by differences in the effects of leaf quality (i.e., resulting from tree diversity) on herbivore performance. Our results show a decrease in herbivore damage with the increase in tree diversity. Additionally, this decrease is not associated with a change in the palatability of the host plants. The results suggest that processes behind the associational resistance are important for our study system. More studies are needed to explain the underpinning processes of the associational resistance.

Population dynamics of forest insects

The population densities of many insects fluctuate not only spatially but also over time (Kendall et al. 1999; Liebhold & Kamata 2000). For long time periods, population densities remain at low levels, but sometimes they reach outbreak levels causing a considerable economic and ecological damage to forest ecosystems (Berryman 1988; Thurber et al. 1994; Webb et al. 1995; Aukema et al. 2011). Some species show periodic fluctuations in the population densities (population cycles) which usually occur in specific habitat patches (Liebhold 1992; Johnsonet al. 2005).

Population dynamics are driven by basic factors that affect rates of mortality and survivorship in species populations (Cornell & Hawkins 1995; Carey 2001). These factors include: (1) natural enemies (Anderson & May 1980; Berryman 1996), (2) the effects of weather (Thomson et al. 1984), (3) interaction with the host plant (Price et al. 1980) and (4) maternal effects (Edelsteinkeshet & Rausher 1989; Ginzburg & Taneyhill 1994). In ecosystems, particularly forests, many factors show co-variation and interact (Wallner 1987; Royama 1997; Hunter & Price 1998). Therefore, attributing processes that control population dynamics to only one factor can be misleading.

Forest insects such as the gypsy moth (*Lymantria dispar* L) and the larch bud moth (*Zeiraphera diniana*) are well studied examples for population dynamics as native and invasive forest pests (Berryman 1991b; Dwyer et al. 2004). The gypsy moth, *Lymantria dispar*, causes severe forest defoliation in its native and invasive ranges and is therefore a species with a high economic relevance. Populations of this insect, like many other foliage-feeding forest insects, exhibit periodic gradations or "population cycles" (Varley et al. 1973; Kendall et al. 1999). Natural enemies, especially parasitoids, are speculated to cause the highest mortality rates within these insect populations (Anderson et al. 1980; Myers 1993; Berryman 1996). However, the actual role of parasitism in population cycles of many forest insects is not well understood. A controversy exists about the actual role of the natural enemies in the population regulation of the gypsy moth, especially in its invasive range (Berryman 1991a; Liebhold & Elkinton 1991).

Studying factors affecting the patterns of population dynamics of forest insects helps us to develop management strategies to predict and control the potential damage of massive defoliations. In chapter four, I review and compare the available information on the factors affecting the population dynamics of the gypsy moth in Europe and other regions of the world. Such factors include natural enemies (parasitoids, predators and pathogens), host plants and weather. I particularly highlight the role of natural enemies in population dynamics of this forest insect.

Dissertation outline

In this dissertation, I highlight the relationship between insects and forests using Lepidoptera as a model species. First, I inspect the role of environmental versus spatial distance processes in the assemblages of forest moths (chapter 2). Second, I investigate the effects of tree diversity on insect herbivory (chapter 3). Third, I review the population dynamics of Lepidoptera insects in forests, with a study on the role of natural enemies. Here, the forest pest, the gypsy moth (*Lymantria dispar* L), is used as a study model (chapter 4). For my studies, I use different methodological approaches ranging from the regional to the local spatial scale and from literature review and statistical data analyses to field assessments and manipulative experiments.

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Chapter 2

Moths in forests: environmental factors versus distance

with Jörg Müller, Hermann Hacker and Roland Brandl

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Abstract

The composition of species assemblages depends on distance between habitats as well as on local environmental conditions. To analyse the species composition of Lepidoptera across 96 strict forest reserves in Bavaria (Germany), covering all natural types of forests in the study region, we first investigated environmental factors that might influence moth richness (α-diversity). Second, we sorted out the relative importance of the environmental and spatial distance on assemblage composition across Bavarian forests (β-diversity) using two statistical approaches. We found that local environmental factors influence species richness at local scales. On larger scales, our results suggested that the distribution and organization of Lepidoptera assemblages across Bavarian forests are controlled by at least two types of ecological processes: local and regional processes. However, the relative importance of these two processes differs between the available methods. The inclusion of traits of species as well as phylogenetic information may help to overcome these methodological issues and to make progress in our understanding of the spatial variation of assemblages.

Keywords: *Assemblages, species compositions, distance approach, raw approach.*

Introduction

Recent hypotheses stressed that biotic interactions (i.e., competition, predation or mutualism), neutral processes and environmental filtering influence the distribution and organization of species assemblages (Hubbell 2001; Pitman et al. 2001; Leibold et al. 2004; Tscharntke & Brandl 2004; Cottenie 2005; Legendre et al. 2005;Tuomisto & Ruokolainen 2006; Peres-Neto & Legendre 2010). Lepidoptera species are active (and passive) dispersers. Thus, the ability to find habitats with suitable hosts and appropriate environmental conditions contribute to the composition of assemblages (Müller et al. 2011). Nevertheless, there is an interaction between the variation of environmental conditions, the dispersal ability of species and other important ecological traits at different spatial scales (Brändle et al. 2000; Komonen et al. 2004; Stefanescu et al. 2011). For example, specialist species are at risk when dispersing outside their habitat. As a result, their assemblage is more closely related to the host composition than the assemblages of generalist species which are often more mobile (Shreeve et al. 2001; Hawkins & Porter 2003; Menendez et al. 2007; Müller et al. 2011). Furthermore, species with a larger body size may have a wider host range and broader habitat niches. Therefore, such species show a higher mobility (Inkinen 1994; Lindstrom et al. 1994; Loder et al. 1998).

The similarity of species assemblages decreases with spatial distance. This process might be a result of neutral processes and the environmental resemblance of nearby habitats (Tobler 1970; Hubbell 2001). In order to disentangle the effects of environment and neutral processes, the distance approach and the raw approach were proposed as alternative statistical methods. Distance approach (plotting the decay of similarity between species assemblages versus geographic or environmental distance) is a useful tool to analyse the relative importance of geographical and environmental distances for the similarity variations among species assemblages (Nekola & White 1999; Tuomisto et al. 2006; Soininen et al. 2007; Astorga et al. 2012). On the other hand, canonical analyses such as variation partitioning are well-known, important tools for modelling communities (Legendre 2008). It helps to study the association among species according to their relationships with environmental and spatial predictors (Peres-Neto et al. 2006; Blanchet et al. 2008; Peres-Neto et al. 2010). However, it is still controversial which method is more powerful to evaluate the roles of spatial distance versus local environmental factors (Tuomisto et al. 2006; Legendre et al. 2008). The controversy mostly focuses on whether these two methods answer the same ecological questions at the same level of data analysis e.g., raw data of species abundances and data of compositional similarity (Legendre et al. 2005; Tuomisto et al. 2006).

In this paper, we study the effects of environment and geographic distance on the variations in the composition of Lepidoptera assemblages across Bavarian forests. First we investigate environmental factors that might influence moth richness in the study sites (α-diversity). Our second, and here most important goal, is to study the effects of environmental factors and geographic distance on the assemblage composition of Lepidoptera (β-diversity) across Bavarian forests by comparing the distance and raw data approaches.

Materials and Methods

Sampling and species matrices

In the strict forest reserves in Bavaria, programs have been launched to monitor assemblages of organisms (Albrecht 1990). The reserves were distributed across all ecoregions in Bavaria ranging from floodplains to alpine forests. Moths from 96 sites were collected between 1980 and 2006 using light traps (Müller et al. 2011). The sampled moths were identified to the species level. From the data we assembled a species x site matrix of abundances. Hellinger transformation was applied on the matrix prior to the statistical analyses. Such transformation provides unbiased estimates of RDA analysis (Legendre & Gallagher 2001; Griffith & Peres-Neto 2006; Peres-Neto et al. 2006).

Explanatory variables

Two groups of environmental indicators were combined to characterize environmental conditions of reserves. The first group included bioclimatic indicators (BIO1: annual mean temperature; BIO11: mean temperature of coldest quarter; BIO12: annual precipitation). The second group contained the mean value of Ellenberg indicators for R: soil reaction; L: light; T: temperature; K: continental climate; F: humidity; N: nitrogen. In addition, we integrated the elevation into the environmental variables as an indicator of microclimate.

The second group of environmental variables was calculated from the vegetation releve´s. Vegetation data were extracted from the unpublished database of the Bavarian State Institute for Forestry. We considered vegetation data collected only within the same time frame as the insect data. In this database, cover abundance of species is recorded on a modified Braun-Blanquet scale, with '+' coding for, 1% cover scale. For further analyses, we recoded this rank scale as follows: r recoded to 0.05%, + to 0.5%, 1a to 2%, 1 and 2 m to 3%, 1b to 4%, 2a to 10%, 2 to 15%, 2b to 20%, 3a to 31%, 3 to 38%, 3b to 44%, 4 to 63%, and 5 to 83%. The sampling effort for plants differed among reserves and ranged from 1 to 137 releve´s (mean=10).

The coordinates of *X*-*Y* (Cartesian) were used for the spatial analysis of the sampling sites. The matrix of distance was calculated using Euclidean distances. The distance between the sites varied between 1 and 379 km.

Data analysis

The effects of environment on species richness

We used the correlation coefficient to study the influence of selected environmental variables on the species richness of moths (α-diversity).

The selection of environmental variables

The selection of environmental variables depended on the best correlation between the composition of Lepidoptera assemblages and environmental variables. To achieve this correlation, we used BIO-ENV in the package vegan, R (Oksanen et al. 2013). This algorithm finds explanatory variables that give the best correlation between assemblage dissimilarities and environmental distances (Clarke & Ainsworth 1993).

Distance decay (β-diversity)

For studying the variations in the assemblage composition of Lepidoptera across the Bavarian forests (β-diversity), we used a simple linear relationship for the Bray-Curtis similarity of species assemblages among the study sites and the spatial distance between these sites (Euclidean distance of the *X*-*Y* coordinates). We also used the same model for the relationship between Bray-Curtis similarity of species assemblages and the environmental distance between the sites (Euclidean distance of the scaled environmental variables). Slope, mean similarity, initial similarity (IS) and half distance (HD) were obtained for the distance decay of the moth communities and spatial distance. The slope in such relationship reflects the rate of distance decay with geographical distance; mean similarity is a good indicator for the compositional similarity of assemblages over all sites. IS reflects the turnover in species composition from site to site. HD reflects the rate of species turnover per unit distance. Long HDs indicate that the rate of species turnover change little with increasing spatial distance, while short HDs show that species turnover (β-diversity) is distance dependent (Nekola et al. 1999; Soininen et al. 2007). The significance of relationships was tested by 999 permutations (Mantel test). We used partial Mantel test for sorting out the relative effects of environmental versus spatial distance (Manly 1997; Legendre & Legendre 1998). First, we applied the test for the environmental distance matrix with the species similarity matrix controlled for the

spatial distance matrix. Second, we exchanged between the environmental matrix and the spatial matrix, while the matrix of species kept constant.

Raw approach

We used principal coordinate analysis for the distance matrix (PCNM) (Borcard & Legendre 2002; Borcard et al. 2004). In order to choose only statistically significant explanatory variables, a forward selection was applied by permutation of species-transformed data and scores of PCNM under a reduced model. In this test, we selected spatial predictors using $P \leq 0.05$ as the threshold. However, we followed the procedure described by Blanchet et al. 2008 to avoid the inflated type I error and the overestimation of the amount of explained variance. Hence, the test for significance of all explanatory was carried out prior to the forward selection and the adjusted coefficient R^2 was used as a stopping criterion (Blanchet et al. 2008). For the environmental explanatory factors, a Principal Components Analysis (PCA) was conducted, and scores were used for the forward selection test. We used the same criteria mentioned above for the forward selection test

The variation partitioning was calculated using Hellinger-transformed species x sites matrix as response matrix; environmental predictors resulted from forward selection as the first explanatory table and spatial predictors resulted from forward selection as the second explanatory table (Griffith et al. 2006; Peres-Neto et al. 2006). All statistical analyses in this study were implemented using functions in packages (vagan and packfor, R) (Dray et al. 2013; Oksanen Jari et al. 2013).

Results

The effects of environment on species richness

The number of moth species ranged between 57 and 752 for the study sites. While moth richness decreased with the increased elevation and precipitation, it increased with the increased temperature (Fig. 1).

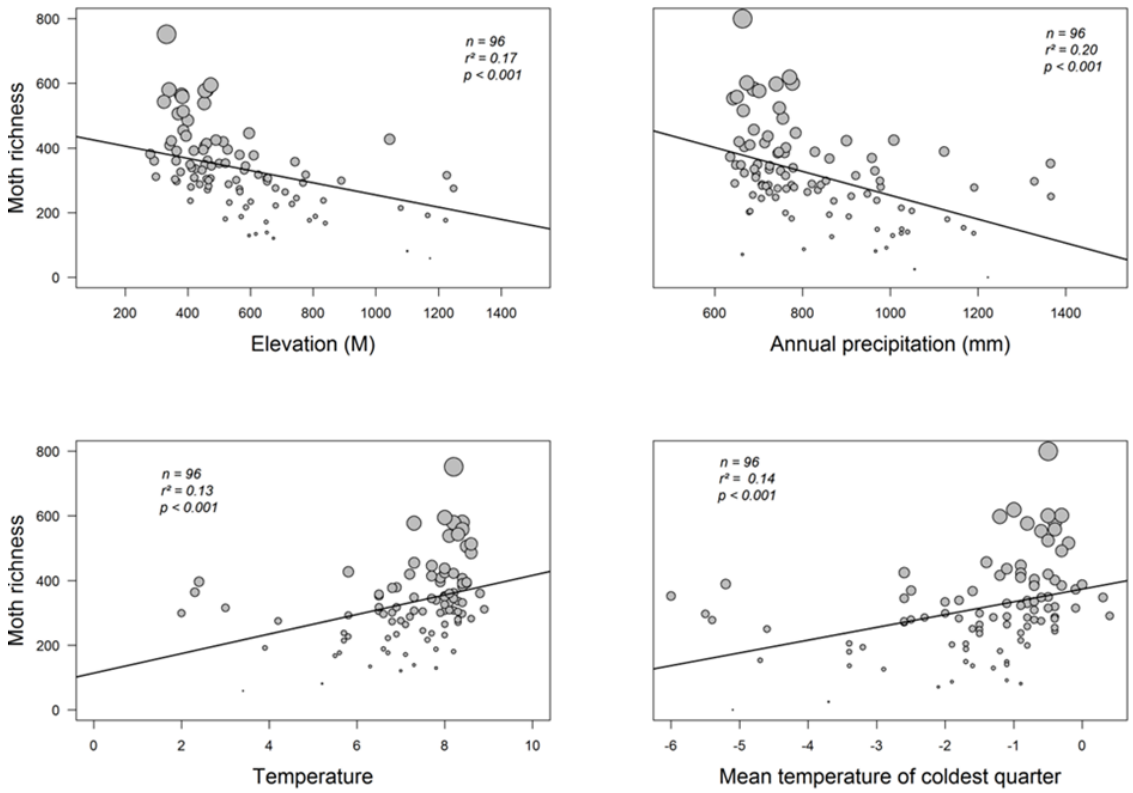

Figure 1 The correlation between moth richness and some environmental variables. The size of the points indicates the relative richness of species according to the site.

Distance decay

A set of five environmental variables that generated the best correlation with the species dissimilarity matrix were selected by BIO-ENV (R^2 = 0.51; for: nitrogen; elevation; annual mean temperature; mean temperature of coldest quarter and annual precipitation).

Mean similarity (0.33) showed that the composition of species assemblages differed considerably across study sites. However, the compositional similarity of moth assemblages decreased with increasing spatial and environmental distance (Fig 2; Table 1). The low rate of the similarity decrease (slope = - 0.0005) and the half distance (HD = 420 km) indicated slow changes in species turn-over at the regional scale. In general, distance decay relationships showed more influence of environment compared to spatial distance on the variation in the compositional similarity of moth assemblages (Table 1). The partial Mantel showed that the variation in species compositions is mainly due to environmental distance (Table 2).

Table 1 Distance decay relationships (spatial and environmental) for the compositional similarity of Lepidoptera assemblages in Bavarian forests

	Lepidoptera	
	Distance	***Environment***
Number of species	**2078**	
Number of sites	**96**	
Mean similarity	**0.33**	
Slope	$-5x10^{-4}$	$-400x10^{-4}$
Intercept	0.41	0.42
Half distance (KM)	420	-
Initial similarity (IS)	0.41	0.38
Mantel R^2	0.19	0.51

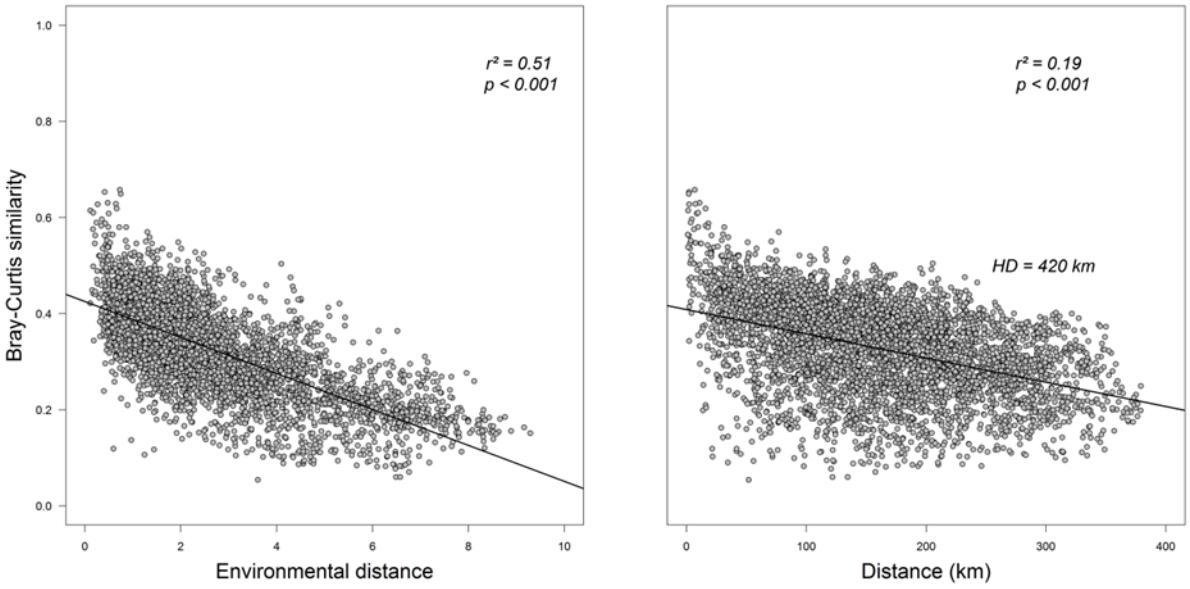

Figure 2 The effects of environment and distance on the community composition of the moths. Half distance (HD): The distance that halves the similarity at one km (Soininen et al. 2007).

In contrast, the variation partitioning showed more influence of the spatial distance than for environment (Table 2). Spatial distance explained 11% of the variance in the composition of moth assemblages. The shared effects explained 6%, while environment explained only 4% of the variation in the moth composition.

Table 2 Dismantling the effects of environment versus the spatial distance on the variations in the composition of Lepidoptera assemblages using two different methods: partial Mantel for linear relationships (distance approach), variation petitioning using adjusted R^2 (raw approach).

Lepidoptera	R^2 distance	R^2 environment	R^2 shared	Residuals
Variation partition	0.11	0.04	0.06	0.79
Partial mantel	0.05	0.42	0.03	0.50

Discussion and conclusions

Our results showed that some local environmental factors (i.e., temperature, precipitation and elevation) correlate to the species richness of Lepidoptera. The local environment of a habitat has been reported to influence species richness of butterflies and moths (Kerr et al. 1998; Brehm et al. 2003; Hawkins et al. 2003; Menendez et al. 2007; Stefanescu et al. 2011). Hence, our results confirm the important role of environment for species richness of Lepidoptera.

For the beta diversity, our results showed that environment and geographic distance affect the variation in species assemblages across Bavarian forests. However, results varied considerably between the two statistical methods. Explaining the role of environment and spatial distance on community composition has recently been highlighted in several ecological studies (Hajek et al. 2011; Astorga et al. 2012). Most of these studies used only one statistical approach to analyse the data. Ours is among the few studies where two statistical approaches (distance and raw) were compared.

The raw and distance approaches explained the variations in the assemblage composition of moth species differently. Therefore, our discussion can follow several lines according to how each method can be interpreted and for which ecological question each method is appropriate: A) If the two statistical approaches (raw and distance) aim at disentangling the effects of environment versus spatial distance on beta diversity, then we might consider one of these methods to be more efficient. We cannot settle this question using the actual data. Nevertheless, simulations showed that the raw approach is efficient from the statistical point of view (Legendre et al. 2008). B) If these methods aim at explaining the variation in species abundances across the study sites, we might consider the raw approach as the more appropriate tool, because it deals with the raw data of species abundances, and it explains variations in raw data, not in the composition of species assemblages (Legendre et al. 2005; Tuomisto et al. 2006; Legendre et al. 2008; Tuomisto & Ruokolainen 2008). Given this framework, geographic distance explained 11% of the variation in moth abundances across

Bavarian forests, while 79% of this variation in species abundances was due to unexplained factors. C) If the methods aim at explaining the variations in the compositional similarity of species (the composition of assemblages), the distance approach might be appropriate (Tuomisto et al. 2006, 2008). Thus, the distance approach suggests that environmental factors explained the variations in the compositional similarity of moth species more than spatial distance across Bavarian forests (Table 2). Irrespective of the conceptual framework, the results of both analyses implied that environment and geographic distance influence assemblages. Furthermore, the considerable residual variation indicates the role of other factors on β-diversity of Lepidoptera.

Local environmental factors influence species richness at local scales. On larger scales, disentangling the ecological processes that affect the composition of species assemblages is of considerable importance to understand the distribution and organization of assemblages. Our results suggested that the distribution and organization of the Lepidoptera assemblages across Bavarian forests are controlled by at least two types of ecological processes: local and regional processes. However, the relative importance of these two processes differs between the available methods. The inclusion of traits of species as well as phylogenetic information may help to overcome these methodological issues and make progress in our understanding of the spatial variation of assemblages.

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Chapter 3

Does insect herbivory on oak depend on the diversity of tree stands?

with Roland Brandl, Harald Auge and Martin Schädler

Submitted to Basic and Applied Ecology

Abstract

Studies on the effects of plant diversity on insect herbivory have produced conflicting results. Plant diversity has been reported to cause positive and negative responses of herbivores. Explanations for these conflicting responses include not only various population-level processes but also changes in plant quality that lead to changes in herbivore performance. In a tree diversity experiment, we investigated the effects of tree diversity on insect herbivory on oak in general and whether the effects of tree diversity on herbivore damage are reflected by the performance (leaf consumption, growth) of the generalist herbivore *Lymantria dispar*. Our study showed that the feeding damage caused by naturally occurring herbivores on oak trees decreased with increasing diversity of tree stands. The performance of *L. dispar* on oak leaves was not affected by tree diversity, neither in field nor laboratory experiments. Our results can be explained by the various processes behind the hypothesis of associational resistance.

Keywords: Tree diversity; Plant-insect interaction; Associational resistance; Plant quality.

Introduction

Plant diversity affects plant–herbivore interactions in a wide range of ecosystems (Coley & Barone 1996; Mulder et al. 1999; Jactel & Brockerhoff 2007; Scherber et al. 2010; Haddad et al. 2011). However, the magnitude and direction of the effects vary considerably among studies. Whilst a number of studies show that herbivore abundance and damage increase with increasing plant diversity (Mulder et al. 1999; Prieur-Richard et al. 2002; Schuldt et al. 2010), other studies demonstrate a decrease in abundance and damage with increasing plant diversity (Scherber et al. 2006; Jactel & Brockerhoff 2007; Unsicker et al. 2008). Some studies indicate that neither abundance of nor damage by herbivores uniformly increases or decreases with plant diversity. Instead, diversity effects are variable and dependent on the identity of the host tree, stand characteristics, as well as the type of herbivores (Vehvilainen et al. 2006; Vehvilainen et al. 2007).

To account for the effects of plant diversity on plant–herbivore interactions, two general hypotheses have been introduced. In the first hypothesis, named "associational susceptibility", an increase in herbivore damage with increasing plant diversity is attributed to a "spill over" of herbivores (White & Whitham 2000; Brockerhoff et al. 2006; Barbosa et al. 2009). In this case, herbivores, especially generalists, develop large populations on preferred host plants before shifting to other plants (Brown & Ewel 1987; Wada et al. 2000; White & Whitham 2000; Jactel & Brockerhoff 2007). Moreover, herbivore performance increases with a diverse diet (Unsicker et al. 2008), which may also increase population growth and therefore abundance. The second hypothesis, "associational resistance", suggests that one or more processes could lead to a decrease in herbivore damage with increasing plant diversity. An increased diversity of plant species might support the abundance and efficiency of natural enemies (Andow 1991). As a result, a decrease of herbivore pressure is expected. Furthermore, herbivores, particularly specialists, are faced with a resource dilution in a diverse plant community (Tahvanainen & Root 1972; Root 1973; Barbosa et al. 2009). Additionally, increasing tree diversity in stands may decrease herbivore pressure due to the higher probability of focal trees being associated with taller neighbours, which decrease the apparency of the focal trees for herbivores (Castagneyrol et al. 2013).

Plant diversity, however, may also influence plant quality (i.e. nitrogen content of leaves), which in turn affects herbivore feeding. Such changes in plant quality may result from modifications of the soil conditions by co-occurring plant species. Numerous studies show that plants growing in monocultures support herbivores more than plants growing in mixed cultures owing to changes in plant quality (Bach 1980a, b, 1981; van Ruijven &

Berendse 2003; Schenk 2006; Marquard et al. 2013). Furthermore, a reduction in plant diversity leads to changes in nutrient ratios and increasing variance in elemental composition of plants, which lead to changes in herbivore reactions (Abbas et al. 2013). This may also be the case in tree stands as it has been shown that total nitrogen uptake is higher in mixed tree communities (Lang et al. 2014).

Experimental studies on the consequences of species diversity on ecosystem properties and processes are, for obvious reasons, often performed with herbaceous plant species (Baeten et al. 2013). Yet trees, in comparison to many herbaceous plants, represent a more stable and predictable resource for herbivorous insects (Tscharntke & Brandl 2004; Vehvilainen et al. 2007). This predictability has even led to the suggestion that some herbivores may adapt to tree individuals (Raubenheimer & Simpson 1992; Ruhnke et al. 2006). Furthermore, the longer life span of trees than of herbaceous plants might cause pronounced effects of diversity for several reasons: a) the long life span allows tree individuals to implement sophisticated defence strategies against herbivores, b) changes in the apparency and light environment of old trees might alter the levels of herbivory and c) old trees may change the abundances and efficiency of natural enemies (Moore & Francis 1991; Tylianakis et al. 2004; Boege & Marquis 2005).

Here we studied the effects of tree diversity on insect herbivory and the performance of a generalist herbivore (*Lymantria dispar*). Our tree diversity experiment allowed us (a) to assess oak leaf damage caused by naturally occurring herbivores in the field and (b) to assess the performance (leaf consumption, growth) of *L. dispar* feeding on oak foliage in both field and laboratory experiments. We evaluated whether herbivore pressure increases or decreases with tree diversity. The herbivore performance data allowed us to evaluate whether the effects of tree diversity on herbivory can be explained by changes in leaf quality.

Material and Methods

Experimental design

The study was conducted using the infrastructure provided by the Kreinitz Tree Diversity Experiment in central Germany (51°23´N, 13°15´E, 110 m above sea level). This diversity experiment was established in fall 2005 on a former arable field abandoned in the 1990s. The experimental site is surrounded by a matrix of mature forest. The experiment was set up in two blocks; each block consisted of 49 plots of 25 m2 (5 m × 5 m) that vary in diversity and composition of tree species. The tree species pool consists of 6 species native to central Europe: common beech (*Fagus sylvatica* L.), common ash (*Fraxinus excelsior* L.), Norway

spruce (*Picea abies* (L.) H. Karst.), Scots pine (*Pinus sylvestris* L.), sessile oak (*Quercus petraea* (Matt.) Liebl.) and small-leaved lime (*Tilia cordata* Mill.). The plots were randomly assigned to 49 treatments representing 6 diversity levels: bare soil (no trees planted), monocultures (of each of the 6 tree species), all possible combinations of 2 species (15 combinations), all possible combinations of 3 species (20 combinations), all possible combinations of 5 species (6 combinations), and all 6 species. In 2005, 30 two-year-old tree saplings were planted in a regular pattern on each plot, with 1.0 m between rows and 0.8 m between trees in a row. The different species were randomly assigned to each planting position; during the first two years, dead individuals were replaced by saplings of the same species and age cohort. In our study, we used the 22 plots in each block that contained individuals of sessile oak. In the study year, oak trees had reached an average height of 1.9 m. Average height of the other species ranged from 0.96 m (beech) to 2.1 m (ash).

Herbivore damage in the field

In July 2009, herbivore damage on oak trees was assessed on all 44 plots with oaks. On each plot, one oak individual was randomly selected. To avoid edge effects, we selected only individuals from the inner area of the plots. We randomly selected two branches from both upper and lower layers of the chosen individual as tree layer has been shown to affect herbivore damage (Raubenheimer & Simpson 1992; Ruhnke et al. 2009). For each branch, we inspected 16–20 leaves for signs of insect herbivory. We counted leaves with damage caused by leaf chewers, hole feeders, gallers, miners, rollers and skeletonizers and the presence of sap-sucking insects. Leaves from the two branches from each layer were pooled, and the percentage of damaged leaves per tree and layer was calculated. In addition to the calculation of total damage, we also calculated the cumulative damage as the sum of the number of leaves of each damage type (values may exceed 100%). Only damage caused by chewers and hole feeders were common enough to allow separate analyses.

The effects of tree diversity on larval performance

The performance (leaf consumption and growth) of the gypsy moth (*Lymantria dispar* L; New Jersey strain) was measured in the field and laboratory. These caterpillars are generalist herbivores that feed on a wide range of tree species (Alalouni et al. 2013). They are highly sensitive to changes in leaf quality and are therefore a suitable integrative indicator for evaluating tissue quality (Barbosa & Greenblatt 1979; for *Quercus robur* see Giertych et al. 2005). Prior to the experiments, groups of 10 larvae were reared on an artificial diet in plastic

boxes (15 × 11 × 6 cm^3). Feeding was stopped one day before field and laboratory experiments.

In the field experiment, we used 3 larvae per plot (132 larvae). Each larva was weighed and then placed on a randomly selected branch of an oak tree on inner areas of the plot. We covered the branch area of each larva with a fine-meshed bag. After two weeks, we measured the final weight of each larva.

In the laboratory experiment, we used 3 larvae per plot (132 larvae). Each larva was weighed and placed into an individual Petri dish (three Petri dishes per plot). We fed the larvae on oak leaves; i.e. oak leaves from the same tree on the same plot on which the larvae in the field were tested. For this experiment, we collected only leaves without any visible signs of herbivory or pathogens from the plots. The breeding room conditions were set to 23–25 °C, 70–75% humidity and a light:dark regime of 18:6 h for the entire experiment. After 5 days, we measured the final weight of each larva. We also estimated the dry mass of consumed leaves by calculating the difference between the dry weight of used leaves before and after feeding. We estimated the water content per plot by weighing four leaves of the tested oak trees in each plot, drying them and then estimating the percentage of water content. Values from the three Petri dishes of each plot were averaged and used as replicates for the analyses.

Statistical analysis of herbivore damage in the field

Tree diversity was represented in five different diversity levels (1, 2, 3, 5, and 6) as described above, i.e. level 1 represented an oak monoculture on the plot, while level 6 represented the combination of all tree species. Diversity was based on the different species combinations (tree composition) such that levels 2, 3 and 5 have different sub-levels based on species combinations. The effect of tree diversity on leaf damage in the field was tested using a generalized linear mixed model with block, tree diversity (categorical), species composition, tree individual and layer as factors. Block, tree individual and species composition were considered as random factors. Species composition was nested within tree diversity, and the upper and lower layers were considered as split-plots within individuals. The model was calculated as a binary response model with logit link function, and linear contrasts were used to test the a priori hypothesis that diversity caused a gradual change of response variables (Proc Glimmix, SAS 9.2).

Statistical analysis of the effects of tree diversity on larval performance

We tested the effects of diversity on the performance of the gypsy moth larvae (leaf consumption, growth) using nested ANCOVAs for both laboratory and field experiments. Again, block and tree composition were included as random effects, and tree composition nested within diversity. To account for initial differences of larvae, initial larval weight was used as a covariate (Type I sum of squares) of final weight and consumed leaf mass (Raubenheimer & Simpson 1992; Ruhnke et al. 2009). For the analysis of biomass gain of larvae, consumed leaf material was used as covariate, giving an estimate of the efficiency of conversion of ingested food into body mass (Waldbauer 1968). Linear contrasts were used to test the a priori hypothesis that diversity caused a gradual change of response variables (Proc Mixed, SAS 9.2). Prior to the analyses, we tested the assumptions of ANOVA (normal distribution, heteroscedasticity) by visual inspection of residuals.

Results

The proportion of oak leaves on both tree layers damaged by herbivores in the field decreased with tree diversity (overall $F_{4, 17} = 2.59$, $P = 0.08$; linear contrast $P < 0.05$; Fig. 1A). The same pattern was found for the percentage of leaves with damage caused by leaf-chewing insects (Fig. 1B; tree diversity: $F_{1, 17} = 2.95$, $P = 0.05$; linear contrast: $P < 0.05$), but not for damage caused by hole-feeding insects (Fig. 1C; tree diversity: $F_{1, 17} = 1.40$, $P > 0.1$).

Leaf damage was not dependent on tree species composition (all $P > 0.1$). Total leaf damage was generally higher in the upper tree layer (lower layer: 39% ± 8.6%; upper layer 49% ± 8.6%; $F_{1, 39} = 16.5$, $P = 0.002$). Damage caused by leaf chewers was also generally higher in the upper tree layer (lower layer: 29% ± 7.9%; upper layer: 42% ± 7.9%; $F_{1, 39} = 27.4$, $P < 0.001$). For hole feeders, the effect of tree diversity was dependent on tree layer (significant interaction: $F_{1, 39} = 6.51$, $P = 0.004$). Only in the lower layer was damage by hole feeders higher in oak monocultures (Fig. 1C).

Tree diversity and composition showed no effects on the larval consumption and growth, neither in the field nor in the laboratory (ANCOVA: $P > 0.1$ for all tests; Fig. 2).

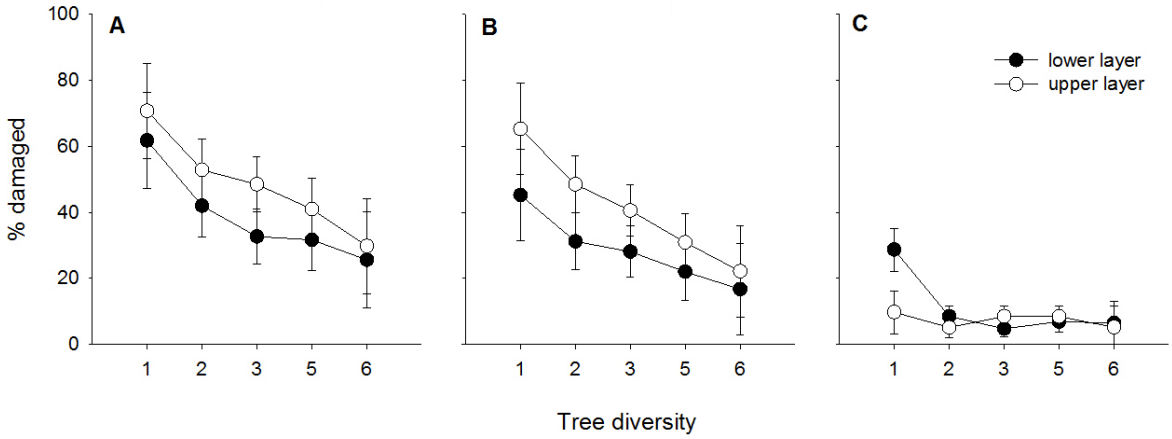

Figure 1 Damage caused by herbivores feeding on oak foliage in the field. A) Total damage, B) damage caused by leaf chewers, and C) damage caused hole feeders. Values are means ± standard errors.

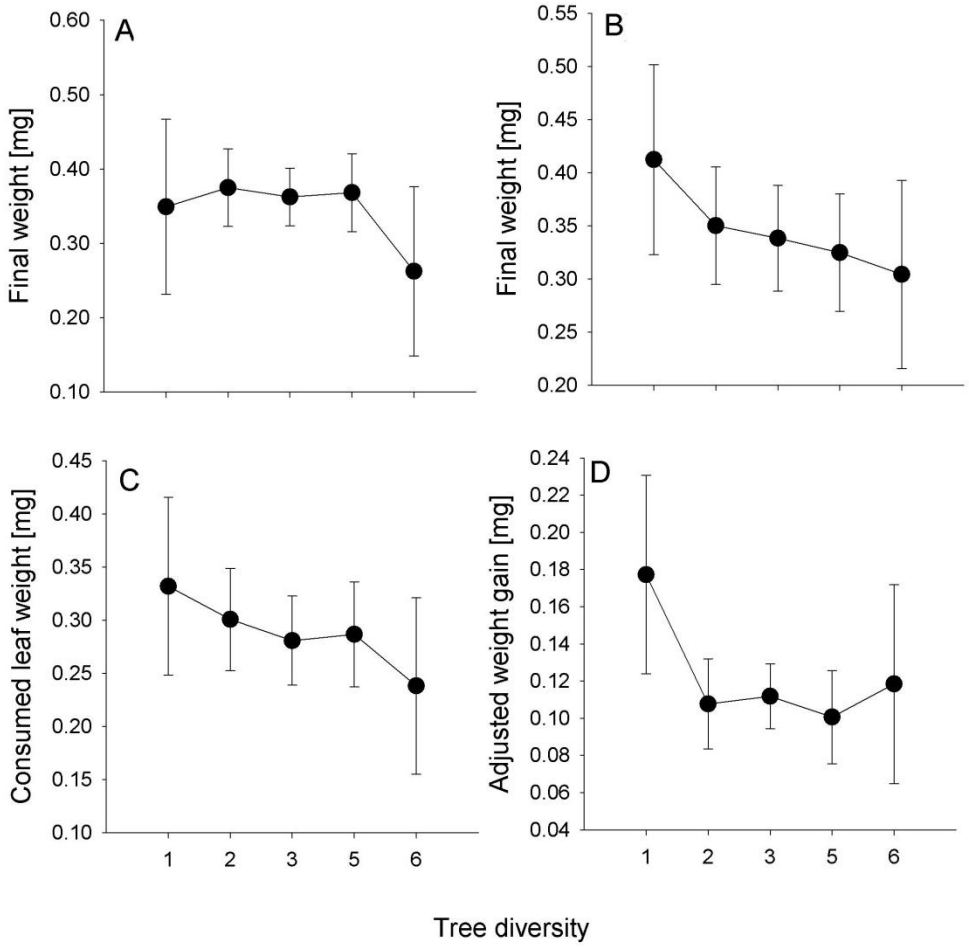

Figure 2 Effects (means ± standard errors) of tree diversity on A) final weight of *Lymantria dispar* larvae feeding on oak leaves, adjusted for the initial weight of larvae, B) final weight of larvae feeding on oak leaves in the laboratory, adjusted for the initial weight of larvae, C) consumed leaf dry weight in the laboratory, adjusted for the initial weight of larvae and D) larval weight gain in the laboratory, adjusted for consumed leaf material. For details, see Materials & Methods.

Discussion

The genus *Quercus* harbours more species of phytophagous insects than any other tree genus in Germany (Brändle & Brandl 2001). This may in part explain the high herbivory damage on leaves observed, with up to about 70% in oak monocultures. Furthermore, we found that an increase in tree diversity was associated with reduction in the total damage caused by herbivores. Our study also showed that tree diversity had no effects on the performance of gypsy moth larvae.

Our results do not support the associational susceptibility hypothesis and suggest that the patterns in herbivore damage in the investigated system are not explained by changes in leaf quality. Thus, the various processes behind the associational resistance hypothesis provide possible explanations for our results. First, control of herbivores by natural enemies (Root 1973; Wilby & Thomas 2002; Sobek et al. 2009) might be involved in the decreased leaf damage observed with increasing diversity of tree stands. Tree diversity might supply natural enemies with appropriate resources and habitats, thereby increasing their efficiency in controlling populations of insect herbivores (Wilby & Thomas 2002; Jactel et al. 2005; Cardinale et al. 2006; Barbosa et al. 2009). Second, tree diversity might divert herbivores, particularly specialists, from their preferred hosts. This disruption involves optical and chemical processes (Floater & Zalucki 2000; McNair et al. 2000; Dulaurent et al. 2012) in which visual and olfactory cues of non-host or less-preferred trees hinder phytophagous insects from finding their host trees (Finch et al. 2003; Reeves et al. 2009; Jactel et al. 2011). Furthermore, a decrease of tree apparency with increasing tree diversity might contribute to the reduction of damage detected in our experiment (Castagneyrol et al. 2013).

Castagneyrol et al. (2014) have demonstrated that the effects of tree diversity also depend on the phylogenetic diversity of tree species mixtures as well as herbivore specialization. In their study, the associational resistance against generalist herbivores is high in phylogenetically diverse tree mixtures, whilst herbivory by specialists is generally low in such mixtures. Our experiment was not designed to test for effects of phylogenetic diversity, but the absence of any significant effects of species composition on herbivory indicated that phylogenetic diversity was of little importance for our results.

Some studies have led to speculations that herbivores should change their performance with changes in plant quality owing to tree diversity (Bach 1980a, b) as well as composition of tree species (Moore et al. 1991). For example, the consumption and growth of a generalist herbivore is significantly greater on oak leaves from experimental oak–spruce mixtures than from oak–alder mixtures or/and pure oak stands (Moore et al. 1991). In our experiment, tree

diversity and composition had no effect on the performance of the gypsy moth larvae. If herbivore performance depends on the quality of the diet, then our results implied that there is no change in plant quality across the experimental levels of tree diversity. But cautionary notes are in order to qualify our findings. First of all, changes in leaf quality (e.g. due to complementary effects of tree mixtures) is expected to increase over time, and the tree stands used for our experiments may have been too young to show such effects (Moore et al. 1991; Boege et al. 2005). Moreover, the performance of herbivores on trees depends not only on leaf quality (Moore et al. 1991) but also on other factors that involve leaf distribution across the canopy, time of bud break, the physical structure and biochemical processes. Plant quality also depends on the genotype and may therefore vary among and within tree individuals (Dudt & Shure 1994; Laitinen et al. 2000; Osier et al.2000; Osier & Lindroth 2001; Henriksson et al. 2003). Clearly, the plethora of factors influencing feeding behaviour and development of herbivorous insects (Osier et al. 2000; Fortin & Mauffette 2002; Osier & Lindroth 2004) might dilute diversity effects.

Results of previous studies have suggested that there is no general pattern of variations in leaf palatability among the various layers of the canopy (Rowe & Potter 1996; Reynolds & Crossley 1997; Fortin et al. 2002; Ruhnke et al. 2009). Such a variation in tissue quality across canopy layers varies not only between tree species and tree individuals, but also between years (Ruhnke et al. 2009), which makes trees “moving” targets for herbivores. In our experiment, we found higher herbivory damage in the upper layers of individual oaks than in the lower layer (except for hole feeders). However, we are not able to offer a specific explanation of this finding, which may range from a higher proportion of young leaves on the upper layer (young leaves have a high nitrogen content and low tannin concentrations) to microclimatic effects (Murakami & Wada 1997; Murakami et al. 2005)

In conclusion, our study showed that damage caused by herbivores decreases with increasing tree diversity, which is in line with several recent studies (Jactel & Brockerhoff 2007; Kaitaniemi et al. 2007). This reduction in tree damage seems to be due to processes that increase associational resistance to herbivores. However, our results provide no insights on the possible mechanisms behind the associational resistance hypothesis. Therefore, further investigations are necessary to analyse the host-search behaviour of herbivores as well as the abundance of natural enemies in relation to plant diversity.

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Chapter 4

Natural enemies and environmental factors affecting the population dynamics of the gypsy moth

with Martin Schädler and Roland Brandl

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Abstract

The population densities of the gypsy moth (*Lymantria dispar*; Lepidoptera: Lymantriidae) may reach outbreak levels that pose considerable economic and environmental impacts to forests in Europe, Asia, Africa, and North America. Compared to the situation in its native European range, feeding damage by gypsy moth is often found to be more severe in North America and other parts of the world. Thus, the release from natural enemies can be interpreted as an important cause for high feeding damages. Natural enemies, especially parasitoids, can cause delayed density-dependent mortality, which may be responsible for population cycles. In North America where only few parasitoids have been introduced and the parasitism rates are considerably lower than in Europe, generalist predators play a larger role than in Europe. Many other factors seem to influence the population dynamics of the gypsy moth such as the host plants and weather. Nevertheless, much of the variability in population densities of the gypsy moth may be attributed to interacting effects of weather conditions and attack by natural enemies. In spite of the considerable number of studies on the ecology and population dynamics of the gypsy moth and the impact of their natural enemies, more quantitative information is required to predict the population dynamics of this pest species and to control its economic and ecologic impact.

Keywords: *population cycles, natural enemies, density-dependent mortality.*

Introduction

World-wide, insect pests affect around 35 million hectares of forests each year (FAO 2010). The gypsy moth, *Lymantria dispar* L, is one of the pest species that can cause considerable problems in forest ecosystems. This foliage-feeding moth occurs naturally from Western Europe to the Central Asia to the Far East and across large parts of the Mediterranean (Giese & Schneider 1979; Grijpma 1989; Pogue & Schaefer 2007; Alalouni 2009; Avci 2009). It was introduced to New Zealand and North America (Glare et al. 1998; Pogue & Schaefer 2007; Orozumbekov et al. 2009). In North America, the species first appeared near Boston around 1868 and expanded its range across most of the north-eastern states in the US and eastern provinces of Canada (Liebhold et al. 1992; Sharov et al. 2002).

In order to understand the factors affecting the abundance and outbreaks of this economically and ecologically important pest, its population dynamics have been modelled to predict population dynamics for the development of management strategies (Campbell 1981; Sheehan 1989; Elkinton & Liebhold 1990; Berryman 1996; Novotny et al. 1998; McManus & Csoka; 2007). The patterns of insect population dynamics are bewildering and are based on various density-dependent and density-independent factors (May 1974; Berryman & Stark 1985; Berryman et al. 1987; Wallner 1987). However, density-dependent factors have the major role in regulating populations (Berryman 1991b, 1996). Since most insect parasitoids act in a density-dependent manner, an understanding of their role in the dynamics of insect pests is important for predicting patterns of population outbreaks in space and time (Royama 1977; Berryman 1996). Data from native and invasive ranges suggest that the natural enemies of the gypsy moth may control its population dynamics (Turchin 1990; Berryman 1991a, b, c, 1998). It has been speculated that the escape from native natural enemies seems to be one reason of the invasion success and therefore higher feeding damages in the new range (Keane & Crawley 2002; Wolfe 2002; Clay 2003; Colautti et al. 2004).

Despite the economic and ecological importance of the gypsy moth, data on its ecology, population dynamics and the importance of its natural enemies are widely scattered in the literature. Here, we review the available information on the gypsy moth for Europe in comparison with other regions of the world. We especially focus on the comparison between natural enemies in the native and the new range of the species. We further complement this with information about host plants in the different parts of the range to account for further factors which may influence population dynamics. The ultimate aim of this study is to stimulate further research on factors that trigger population and outbreak dynamics of this ecologically and economic important pest species.

Population dynamics and outbreaks of the gypsy moth

The gypsy moth has univoltine life cycle which affects its population dynamics (Montgomery & Wallner 1988). The insect diapauses in winter as an egg mass. Neonate larvae play a major role in the natural dispersal of the population through ballooning (Barbosa & Capinera 1978; Pogue & Schaefer 2007). While males have five instars, females usually have six which extends their period of exposure to natural enemies (Grijpma 1989). The pupae require approximately 2 weeks for development providing an ample opportunity for parasitoids and predators to attack (Leonard 1981).

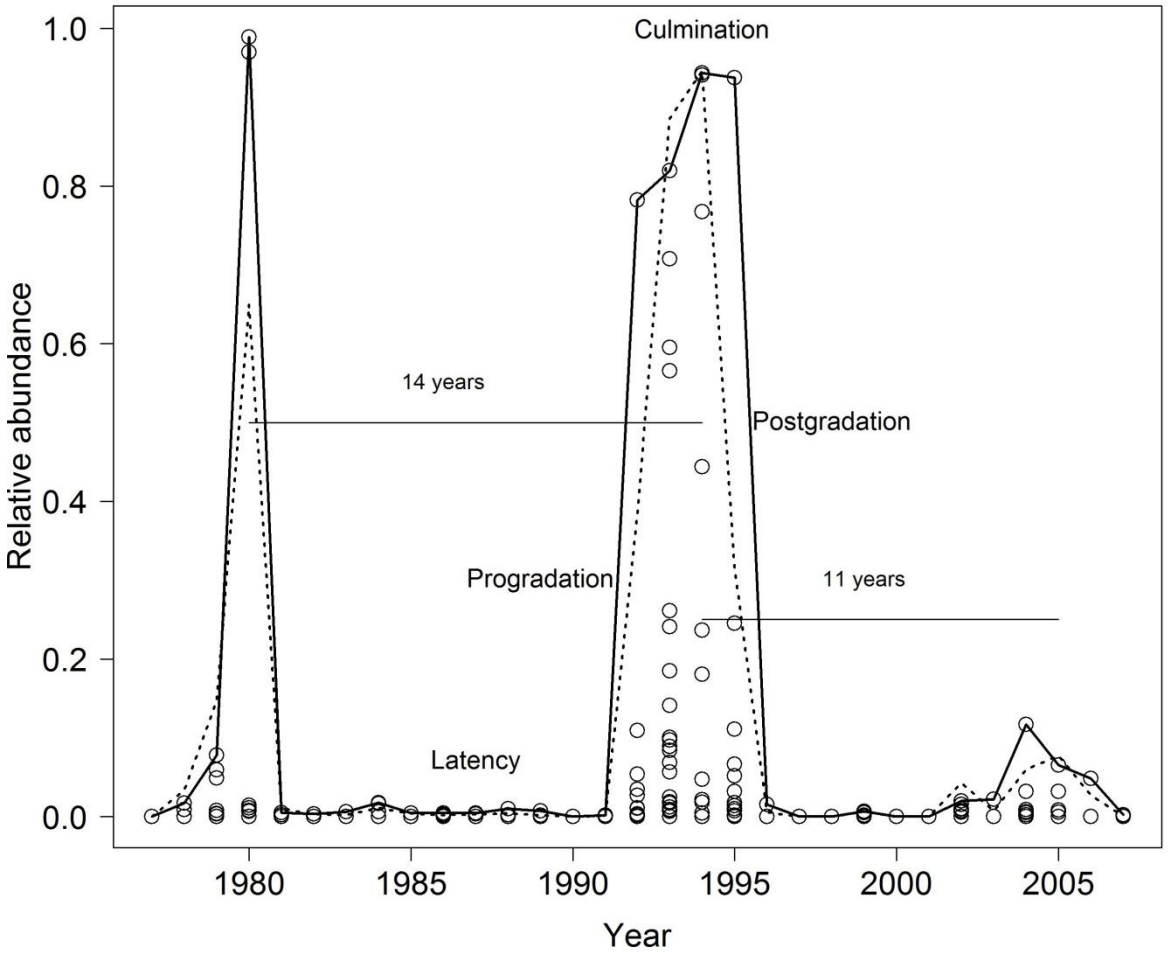

Figure 1 Change of the relative abundance of Gypsy moth in southern Germany to illustrate the terms used to describe the various phases of the population cycle. Open circles: relative abundance of gypsy moth to other moth species across sites; solid line: maximum density; dotted line: mean values (multiplied by 30). The insect needs three years to reach the culmination from the beginning of progradation period. (Hacker, unpublished data; see also Müller et al. 2011)

Populations of the gypsy moth, like many other foliage-feeding forest insects, exhibit periodic gradations or population cycles (Varley et al. 1973; Leonard 1974; Berryman 1996; Kendall et al. 1999). These gradations seem to be localized at certain centres where conditions are presumed to be favourable. For example, cycles have occurred in the same forests of birch and alder in western Lithuania every ten years since the 1970s (1971–1975, 1982–1983, 1993–1994; Zolubas et al. 2001). In Europe, the following terms are used to describe the various phases of the cycle (see fig. 1): latency (when population is at low levels of density), pro-gradation (population starts to erupt), culmination or outbreak (population reaches high levels of density), and postgradation or retrogradation (population density decreases after outbreaks) respectively (Campbell 1981; Montgomery & Wallner 1988; Elkinton & Liebhold 1990; fig. 1). In North America, ecologists use the terms (innocuous or endemic, release phase, outbreak phase and decline phase (Elkinton & Liebhold 1990). The number of the egg masses per unit ground area or per tree in the spring before the hatch time usually gives an indicator of the gradation phase (Liebhold et al. 1994). The size of the egg masses and the proportion of the old egg masses can also give indications for the population phase (for more details see also Liebhold et al. 1994).

The outbreaks of gypsy moth populations seem to be synchronized across large scales (Myers 1998; Johnson et al. 2005). Fifteen European countries (Austria, Czech Republic, France, Germany, Hungary, Italy, the Netherlands, Poland, Portugal, Russia, Spain, Romania, Serbia, Slovakia and Switzerland) experienced outbreaks between 1990 and 1995. Even small outbreaks occurred during this period in England, where the climate is rather unfavourable for this insect (Lipa & Kolk 1995; Wulf & Giraser 1996; Narang et al. 2001; Cannon et al. 2004). However, there are some regional differences in the time span of two outbreaks, for example, in Slovakia and Germany; the period between two outbreaks can differ from 6 to 14 years (Grijpma 1989; Novotny et al. 1998; Delb 1999; Turcani et al. 2003b; see also fig. 1). The time between outbreaks' events can also vary across latitude and longitude (Weiser 1987; McNamara 1996). A period of three to four years between two outbreaks was observed in the Mediterranean and Balkan regions, whereas average of seven to ten years was observed in Central Europe (Weiser 1987; McManus & Solter 2003). The damage caused by the insect in the Mediterranean and Balkan is more severe as well. The warmer and drier climate which provides larvae with favourable conditions for development and survival might explain this short and intensive outbreak cycles (Grijpma 1989; Weiser 1987; McManus & Solter 2003). Furthermore, forest type (xeric soil, host plants) might shorten the cycle of outbreak compared with Central Europe.

In North America, the population dynamics of the gypsy moth were described in various terms, such as bimodal dynamics, population cycles, second-order lag correlations, and spatial synchrony (Campbell & Solan 1976; Montgomery & Wallner 1988; Liebhold 1992; Liebhold et al. 2000). In early studies, the evidence for cyclic fluctuations of population densities was not convincing in North America (Elkinton & Liebhold 1990; Liebhold & Kamata 2000). More recent studies, however, found population cycles with periods of five and ten years between two outbreaks. Moreover, the period between two outbreak events differed with respect to the forest type (xeric, mesic; Johnson et al. 2005; Haynes et al. 2009; Bjornstad et al. 2010).

Explanations for why some foliage-feeding insects have population cycles have been widely discussed (Turchin 1990; Berryman 1991a, c; Murray 1999; Liebhold & Kamata 2000; Carey 2001). Many hypotheses have been proposed to explain this phenomenon, for example, maternal effects, changes in population genetics and the effects of host plant quality (Chitty 1967; Edelsteinkeshet & Rausher 1989; Ginzburg & Taneyhill 1994; Liebhold & Kamata 2000; Liebhold et al. 2000). Nevertheless, the delayed density-dependent mortality caused by natural enemies was supposed to be the main reason for population cycles in gypsy moth populations (Turchin 1990; Berryman 1991a, b; Liebhold & Elkinton 1991; Liebhold & Kamata 2000). In Central Europe, larval and pupal parasitoids can control abundance during outbreaks and postgradations (Maier 1995; Hoch et al. 2001; Turcani et al. 2001). Furthermore, some tachinid parasitoids have generation times similar to that of their host. Thereby, the progradation phase seems to be a result of the escape from these enemies (Montgomery & Wallner 1988; Berryman 1991b, 1996, 1998). In North America, rates of parasitism by tachinids are lower than in Europe. In spite of that, a delayed density dependence caused by introduced parasitoids was proposed as a factor controlling gypsy moth populations (Berryman 1991a, b, 1998). No evidence was found to support this proposal (Liebhold & Elkinton 1991; Liebhold et al. 2000). On the other hand, predation by small mammals appears to be the major cause of mortality in low-density populations, which slows down the increase of gypsy moth populations to outbreak levels (Liebhold et al. 2000). These observations led to the proposal that the changes in the density of generalist predators might be a determinant of the outbreak events (Liebhold et al. 2000; Johnson et al. 2006; Bjornstad et al. 2010). A recent study of the gypsy moth population cycles in North America suggested that even in the absence of the strong environmental changes, the behaviour of the gypsy moth population is controlled by trophic interactions (Allstadt et al. 2013).

The effects of natural enemies on population dynamics

The gypsy moth encounters a diverse complex of natural enemies (Hoch et al. 2001). However, the effect of these enemies varies depending on the phase of gradation (Novotny 1989; Maier 1990, 1995; Novotny et al. 1998; Hoch et al. 2001; Turcani et al. 2001). More than 150 species of parasitoids are able to attack the gypsy moth in Europe (109 Hymenoptera, 56 Diptera; Grijpma 1989). The parasitism rates vary between 10 and 100% (Reardon 1981a). Despite this pool of parasitoids, efforts to establish parasitoids in the invasive range of the gypsy moth have been only partially successful, and only few parasitoid species can be considered as established (Campbell 1976; Reardon 1976; Montgomery & Wallner 1988; Glare et al. 1998).

Egg parasitism

The gypsy moth egg parasitoids and hyperparasitoids have been recorded from six different families of Hymenoptera (Brown & Cameron 1982; table 1). *Anastatus japonicus* (Eupelmidae) and *Ooencyrtus kuvanae* (Encyrtidae) are considered the most important egg parasitoid species in Central Europe (Grijpma 1989). Other parasitoids including *Anastatus catalonicus*, *Anastatus bifasciatus*, and *Anastatus japonicus* are important, for example, *A. catalonicus* attacked 40% of one egg mass in Germany (Maier 1995). *O. kuvanae*, *Anastatus disparis* and *A. bifasciatus* attack egg masses in Turkey, but *O. kuvanae* causes higher mortalities than the other two species (Avci 2009). The parasitism rates of egg parasitoids seem to fluctuate considerably in the native range of the gypsy moth. The rates vary between 0 and 10% in Central Europe and can reach more than 60% during an outbreak in Turkey (Maier 1995; Bathon 1996; Hoch et al. 2001; Turcani et al. 2001; Avaci 2009). These data suggest that parasitism rates decrease with latitude (fig. 2a). Moreover, there is no correlation between the density of egg masses and parasitism rates in the native range, and the parasitism rates seem to be higher in repeatedly infested than in recently infested forests (Bathon 1996; Hoch et al. 2001; Turcani et al. 2001; Avci 2009).

In Asia (Korea and Japan), egg parasitoids seem to have little importance (Brown 1984; Schaefer et al. 1988). In North America, *A. disparis* and especially *O. kuvanae* are considered the main parasitoids of egg masses (Hoy 1976; Reardon 1981b). Together their parasitism rates can reach 20 to 40% (Brown & Cameron 1982; Brown 1984; McManus & Coska 2007). Although it is considered to cause higher mortality than *A. disparis*, *O. kuvanae* shows an extreme variability in parasitism rates as a result of the dependence on the size of the egg masses (Brown et al. 1983; Brown 1984).

Table 1 The main invertebrate parasitoids and predators of the gypsy moth egg mass. Information compiled from (Brown & Cameron 1982; Mason & Ticehurst 1984; Villemant & Ramzi 1995; Hoch et al. 2001; Turcani et al. 2001, 2003b; Avaci 2009; Camerini 2009).

	Order	Family and Parasitism rates*	Species
Parasitoids	Hymenoptera	Encyrtidae	*Ooencyrtus kuvanae*
		10–20% Central Europe and North America	
		Eupelmidae	*Anastatus disparis*
		10–20% Europe	*Anastatus bifasciatus*
			Anastatus japonica
			Anastatus catalonicus
		Scelionidae	*Telenomus* sp.
		Torymidae	*Torymus anastativorus*
		Eulophidae	*Atoposomoidea ogimae*
		Pteromalidae	*Dibrachys cavus*
		Eulophidae	*Pediobius* sp.
Predators	Hymenoptera	Formicidae	*Aphaenogaster rudus rudus*
			Aphaenogaster tennesseensis
			Crematogaster cerasi
	Coleoptera	Dermestidae	*Dermestes lardarius.*
		1–10% North America	*Trogoderma versicolor*
		10–90% North Africa	*Anthrenus vladimiri*
			Megatoma undata
			Cryptorhopalum ruficorne
		Trogossitidae	*Tenebroides maroccanus*
	Hemiptera	Pentatomidae	*Podisus* spp.

* Rough estimates of the parasitism's rates. These rates might vary considerably due to different factors.

At present, the available information allows no clear conclusions about the influence of egg parasitoids on the population dynamics of the gypsy moth. More comparative studies about the influence of egg parasitoids in the native and new range of the insect are needed.

Larval and pupal parasitism

More than 23 species of parasitoids and hyperparasitoids have been recorded in Slovakia, Austria and Germany (table 2; Bathon 1993; Maier 1995; Hoch et al. 2001; Eichhorn 1996; Turcani et al. 2001). The tachinids *Parasetigena silvestris* and *Blepharipa sp.* cause the highest mortality rates. Together these species are the dominant tachinid parasitoids in Austria, Germany, Lithuania, Poland and Slovakia (Maier 1990, 1995; Eichhorn 1996; Hoch et al. 2001, 2006; Turcani et al. 2001; Zolubas et al. 2001; Sukovata & Fuester 2005). These two species are specialized and univoltine which make their life span similar to their host (Montogomery & Wallner 1988; Maier 1990). While *B. pratensis* place the egg on the consumed foliage, *Parasetigena silvestris* place it directly on old larvae resting in the trunk flaps (Odell & Godwin 1984; Gould et al. 1992). Therefore, the number of host-damaged leaf clusters and density of larvae significantly enhance oviposition and consequently the response for the changes in the host density (Odell & Godwin 1979, 1984; Williams et al. 1992). Other species of tachinids such as *Exorista* spp and *Compsilura* spp also are common in Europe. *Exorista segregate*, *Compsilura concinnata* and other species caused 20% of mortality for larvae and pupae during an outbreak period in Turkey (Avci 2009). *C. concinnata* also parasitized the gypsy moth during a period of low density in Italian willow forests (Camerini 2009).

Other important species that mainly belong to Braconidae, Ichneumonidae and Chalcididae also cause high rates of parasitism, but usually at low or increasing population levels (Maier 1995; Bathon 1996; Schopf & Hoch 1997; Hoch et al. 2001; Turcani et al. 2001; Zolubas et al. 2001). *Glyptapanteles liparidis* and *Glyptapanteles porthetriae* seem to be abundant in latency and progradations in Europe (Schopf & Hoch 1997; Hoch et al. 2001; McManus & Csoka 2007). *Phobocampe* sp. of the family Ichneumonidae cause considerable parasitism rates for the larvae and pupae in postgradations (Maier 1995; Zolubas et al. 2001). These species are oligo- or multivoltine. They are also not specific to the gypsy moth which makes them less respondent to the changes in population densities and more active in low density populations. For example, *Glyptapanteles liparidis* has excellent searching capacity, which makes this species effective in low density and in areas where populations increase (Schopf & Hoch 1997). However, like the other parasitoids, many factors influence the relationship between this gregarious endoparasitoid and the larvae. Such factors include: larval age, alternative hosts, host size and parasitoids complex (see also Schopf 1991; Schopf & Rembold 1993; Schopf & Steinberger 1996).

Table 2 Main parasitoids of the larvae and pupae of the gypsy moth. Information compiled from (Montogomery & Wallner 1988; Elkinton & Liebhold 1990; Maier 1990, 1995; Pemberton et al. 1993; Eichhorn 1996; Hoch et al. 2001, 2006; Turcani et al. 2001; Lee et al. 2002; Avaci 2009; Camerini 2009; Lee & Pemberton 2009)

Order	Family	Species
Diptera	Tachinidae	*Parasetigena silvestris* (Rob.-Desv)
		Blepharipa pratensis (Meigen)
		Compsilura concinnata (Meigen)
		Zenillia libatrix (Panzer)
		Siphona borealis (Mesner)
		Blepharipa schineri (Mesnil)
		Palexorista sp.
		Carcelia gnava (Meigen)
		Drino incospicua (Meigen)
		Senometopia separata (Rondani)
		Exorista lavarum (L.)
		Exorista segregate (Rondani)
		Aphantorhaphopsis samarensis (Villeneuve)
		Pales pavida (Meigen)
	Sarcophagidae	*Parasarcophaga uliginosa* (Kramer)
Hymenoptera	Braconidae	*Apanteles xanthostigma* (Haliday)
		Glyptapanteles liparidis (Bouché)
		Glyptapanteles porthetriae (Muesebeck)
		Cotesia melanoscela (Ratzeburg)
		Meteorus pulchricornis (Wesmael)
		Cotesia ocneriae (Ivanov)
		Apanteles sp.
		Rogas sp.
Hymenoptera	Ichneumonidae	*Gelis areator* (Panzer)
		Hyposoter tricoloripes (Viereck)
		Phobocampe lymantriae (Gupta)
		Phobocampe unicincta (Gravenhorst)
		Phobocampe disparis (Viereck)
		Pimpla hypochondriaca (Ratzeburg)
		Lymantrichneumon disparis (Poda)
		Theronia atalantae (Poda)
	Chalcididae	*Monodontomerus* sp.
		Brachymeria intermedia (Nees)

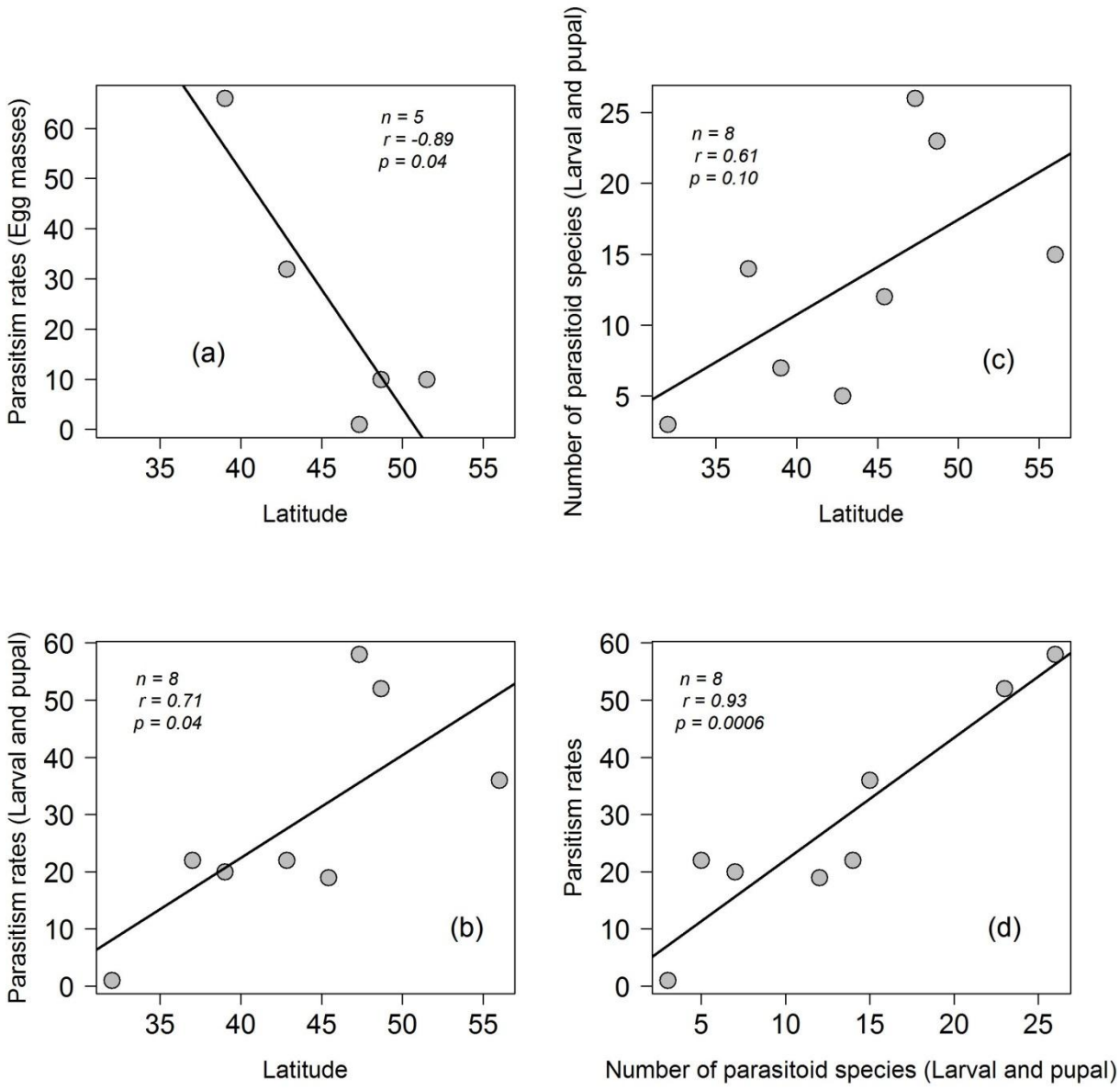

Figure 2 Relationship between latitude and parasitism rates of the gypsy moth. (a) Correlation between latitude and the percentage of egg parasitism; (b) correlation between latitude and the rates of larval and pupal parasitism; (c) correlation between latitude and the number of insect species that parasitize the gypsy moth; and (d) correlation between the number of parasitoid species that attack the gypsy moth and the parasitism rates. For these plots we collected information from different studies for different areas in the world (e.g. Germany, Slovakia, Turkey…etc.). However, we have to acknowledge that the phase of infestation, the sampling method and forest tree compositions are different between the different studies which may strongly influence this analysis. (Data sources: Bathon 1993, 1996; Pemberton et al. 1993; Maier 1995; Eichhorn 1996; Hoch et al. 2001; Zolubas et al. 2001; Lee et al. 2002; Turcani et al. 2003a,b; Avaci 2009; Camerini 2009; Lee & Pemberton 2009; Saeidi 2011).

In the Asian range of the gypsy moth, tachinids, braconids and Ichneumonids comprise most of the parasitoid complex of the larvae and pupae (Lee et al. 2002; Lee & Pemberton 2009). Similar to Europe, the two species of tachinids *P.silvestris* and *Blepharipa* sp. are the most effective parasitoids. On the other hand, *Phobocampe* spp. (Ichneumonidae) are considered effective parasitoids sometimes even more than tachinids (Pemberton et al. 1993; Lee & Pemberton 2009). A recent study in Central Asia showed that tachinids (e.g. *C. concinnata*, and *Exorista larvarum*) do not play a large role in controlling high density populations of *L. dispar* in orchards (Saeidi 2011). However, reports from that region are scarce. In North America, the established parasitoids such as *P. silvestris* and *Blepharipa* spp., and braconids, such as *Cotesia melanoscela* can cause considerable mortality rates (Elkinton & Liebhold 1990; McManus & Csoka 2007).

The existing studies and reports agree that the tachinids species play a major role in the dynamics of the gypsy moth due to the high mortality they cause. They can reduce the density during outbreak significantly. Furthermore, parasitism rates on the larvae and pupae of the gypsy moth seem to increase towards northern latitudes (fig. 2b, 2c, 2d). Montgomery and Wallner (1988) noticed that the response of tachinid species to the change in the gypsy moth density is delayed which might explain the high density of them in postgradations. During low densities of gypsy moth other generalist parasitoids might have the major role to keep population from eruption (table 3).

Predation

The populations of many phytophagous insects are largely determined by their predators and hosts (Price et al. 1980; Wallner 1987). Predators are often generalists that feed on a wide range of prey species. Therefore, it is difficult to determine the impact of predator species on prey populations (Smith 1985; Liebhold et al. 2000). The relative importance of predation on the population dynamics of the gypsy moth seems to differ according to the attacked stage of the insect (egg masses, larvae or pupae), characteristics of predators, forests type and climate. Nevertheless, egg predation by invertebrates is considered to be one of the main factors influencing the population dynamics of the gypsy moth in North Africa (Flaval & Villemant 1997). Seventeen insect species feed on egg masses in cork oak forests in Morocco causing mortalities between 25 and 90%. The climatic conditions combined with the biological and trophic characteristics of the predators enable them to attack egg masses during the 9-month egg stage (Villemant & Ramzi 1995; Villemant & Andrei-Ruiz 1999).

Table 3. Important parasitoids of the larvae and pupae during various population phases in middle Europe and some parts of Asia. The values in the table represent the range between the lowest (zero value means that these parasitoids can be absent in some phases or regions) and the highest possible parasitism rates. (Pemberton et al. 1993; Maier 1990, 1995; Eichhorn 1996; Schopf & Hoch 1997; Hoch et al. 2001, 2006; Turcani et al. 2001; Zolubas et al. 2001; Lee et al. 2002, Avaci 2009; Camerini 2009; Lee & Pemberton 2009)

Population phase	Species	Span of parasitism rates (%)
Latency	*Parasetigena silvestris*	0 -20
	Blepharipa sp.	0-17
	Glyptapanteles liparidis	0-47
	Glyptapanteles porthetriae	0-28
	Cotesia melanoscela	0-25
	Hyposoter tricoloripes	0-14
	Phobocampe sp.	0-10
Prograd ation	*Parasetigena silvestris*	0-77
	Blepharipa sp.	0-57
	Glyptapanteles liparidis	0-23
	Glyptapanteles porthetriae	0-10
	Hyposoter tricoloripes	0-20
	Phobocampe sp.	0-21
Outbreak	*Parasetigena silvestris*	0-95
	Blepharipa sp.	0-65
	Glyptapanteles liparidis	0-18
	Glyptapanteles porthetriae	0-18
	Cotesia melanoscela	0-59
	Phobocampe sp.	0-24
Postgradation	*Parasetigena silvestris*	0-97
	Blepharipa sp.	0-95
	Phobocampe sp.	0-22

Among invertebrates, both the adults and larvae of *Calosoma sycophantha* (Carabidae) are the main predator of larvae and pupae of the gypsy moth (Weseloh 1993, Weseloh et al. 1995; McManus & Coska 2007). In Germany, Austria and Slovakia, the abundance of coleopteran predators increase with the increase in gypsy moth populations (Bathon 1996; Hoch et al. 2006). However, the role of beetles in regulating the populations of the gypsy moth needs more attention (Weseloh 1985a, b; Montgomery & Wallner 1988; Elkinton & Liebhold 1990).

In Europe, vertebrates probably cause more mortality than invertebrates (i.e. in Slovakia, invertebrates caused 38% of the egg mass predation, whereas vertebrates caused 62%; Turcani et al. 2003a). Birds seem to be the most important predators (Reichart 1959; Higashiura 1989; Turcani et al. 2001, 2003a). For example, 77% of the egg masses are damaged in Slovakia (Turcani et al. 2001). In Japan, bird predation on egg masses varied between 4 and 70% and was density independent (Higashiura 1989).

In North America, invertebrate predators of egg masses seem to be not important as a mortality factor. Dermestids (*Cryptorhopalum ruficorne*) can attack 3–10% of the egg masses (Mason & Ticehurst 1984). Predation by vertebrate seems to be more effective, for example, predation rates of egg masses by birds are between 65 to 89% (Cooper & Smith 1995; McManus & Csoka 2007).

Small mammals seem to have an important impact on populations of the gypsy moth. Mice cause high mortalities, for example, 98% of deployed gypsy moth pupae were destroyed within 72 h in Ukraine (McManus & Csoka 2007). Mice also caused more than 45% mortality in an artificial population of gypsy moth pupae in Austria (Gschwantner et al. 2002). The predation by small mammals also plays an important role in gypsy moth dynamics in natural oak forests in Asia (Liebhold et al. 1998). Nevertheless, the abundance of small mammals and predation rates are affected by forest types and elevation (Liebhold et al. 1998, 2005). In general, data from Europe and Asia suggest that predation by small mammals is able to keep gypsy moth populations at low density levels (Liebhold et al. 1998; Gschwantner et al. 2002).

Predation by small mammals is considered one of the most important factors affecting the population dynamics of the gypsy moth in North America (Campbell 1975; Campbell & Solan 1977; Elkinton et al. 1989; Grushecky et al.1998; Hasting et al. 2002). It seems that mammals do not regulate the populations in a density-dependent fashion. The predation rate is mostly determined by the variation in predator densities which is closely linked to the production of acorns (the major food for predators in winter) and not by the gypsy moth densities (Elkinton et al. 1989, 1996; Jones et al. 1998; Liebhold et al. 2000). Furthermore, the

distribution and abundance of small mammals are determined by forest types and elevation among other factors (Yahner & Smith 1991). If small mammal predators are abundant, they are able to control the populations of the gypsy moth at low densities, but this is not sufficient to induce population collapse during outbreaks or to control increasing populations of the insect (Elkinton et al. 1996; Liebhold et al. 2000). Thus, density fluctuations of small mammal predators might be a probable factor of the synchronization in gypsy moth populations. Overall, the available information suggests that the density of small mammal predators along with the proportion of susceptible tree species is an important factor for the gypsy moth population cycles (Sharov & Colbert 1996).

Pathogens

Entomopathogenic microorganisms have a considerable impact on Eurasian populations of the gypsy moth (Weiser 1987, 1998; Novotny 1989; table 4). In Central Europe, the mortality caused by pathogens is higher than the mortality caused by parasitoids (Bathon 1993; Hoch et al. 2001; Turcani et al. 2001). Probably the often reported unknown mortality factors are due to pathogens. For example, the average mortality caused by unknown factors in a six-year study in Slovakia was 24%, which was larger than any other factor (Turcani et al. 2001). Microsporidia and pathogens such as fungi, bacteria, and nematodes also have an effect on European populations of the gypsy moth (Weiser 1998; Maddox et al. 1999; Solter et al. 2009). In the Asian native range of the gypsy moth, fungi may cause epizootics in *L. dispar* populations. Mixed infections of *Entomophaga maimaiga* and *Paecilomyces canadensis* were found in 20% of the dead larvae in Japan (Aoki 1974; Hajek 1999). In North America, the nuclear polyhedrosis virus (NPV) is the most important factor causing the collapse of gypsy moth populations (McManus & Csoka 2007). *E. maimaiga* also caused a dramatic epizootic in larval gypsy moth populations throughout many areas of the north-eastern United State (Andreadis & Weseloh 1990; Hajek et al. 1990).

The significance of pathogens depends on the density of the gypsy moth. During outbreaks NPV infect stressed larvae causing high mortality (Campbell & Podgwaite 1971; Novotny 1989). Therefore, high densities of larvae, non-preferred hosts, and a moist and cold climate are optimal conditions for the virus (Wallis 1957; Campbell & Podgwaite 1971; Murray et al. 1989; Woods et al. 1991). Moreover, most NPV infections start from a few egg masses. Thereafter, the contaminated environment is the major factor for trans-generational transmission (Doane 1970; Woods & Elkinton 1987; Murray & Elkinton 1989).

NPV is an important mortality factor of the gypsy moth in the native and invasive ranges. It causes the collapse of the population during the outbreaks and its effects decrease in low populations. No evidence was found to support the hypothesis that the interaction between the larva and the virus is the reason for population outbreaks (Vezina & Peterman 1985; Bowers et al. 1993).

Table 4 The most important pathogens of gypsy moth larvae (Hajek et al. 1990; Novotny et al. 1998; Weiser 1998; Hoch et al. 2001; McManus & Solter 2003; Turcani et al. 2003a, b; Pirlaska et al. 2006; Saeidi 2011)

Pathogen	Type of organism	Geographic area
Nuclear polyhydrosis virus (NPV)	Virus	North America, Europe, Asia
Bacillus thuringiensis var. kurstaki	Bacterium	North America, Europe, Asia
Entomophaga maimaiga (Humber, Shimazu, and Soper)	Fungus	North America, Eastern Europe
Entomophthora aulicae (Reich)	Fungus	Europe
Beauveria bassiana	Fungus	Central Asia
Nosema muscularis (Weiser)	Microsporidium	Europe
Nosema lymantriae (David and Weiser)	Microsporidium	Europe
Thelohania similis (Weiser)	Microsporidium	Europe
Thelohania disparis (Timofejeva)	Microsporidium	Europe
Plistophora schubergi (Zwölfer)	Microsporidium	Europe

The effects of other factors

Host plants

More than 300 tree species of different families serve as host plants of the gypsy moth (Grijpma 1989; Liebhold et al. 1995). Many of the tree species belonging to families of Fagaceae, Salicaceae, Betulaceae, and Rosasceae are the hosts throughout the native and invasive ranges (Lechowicz & Mauffette 1986; Pogue & Schaefer 2007). The preference of tree species by larvae varies considerably owing to the regional and local composition of the vegetation (Lechowicz & Jobin 1983; Mauffette et al. 1983; Mauffette & Lechowicz 1984). In Central Europe, the primary hosts of the gypsy moth are *Quercus petraea*, *Quercus cerris* and *Quercus robur* (Fagaceae) (Bogenschutz et al. 1989; Grijpma 1989; Twery 1990). In the Balkans and the Mediterranean areas (Spain, Portugal, Sardinia and the southern regions of

France), other species of this genus i.e., *Quercus suber*, *Quercus pubescens* and *Quercus ilex*, are the primary hosts (Serrão 2002; McManus & Csoka 2007). Near the northern limits of its range, in Lithuania, birch (*Betula* spp.) and alder (*Alnus* spp.) are the primary hosts (Zolubas et al. 2001). *Salix alba* is attacked in the southern range margins (Italy; Camerini 2009). There further seems to be a current trend towards an expansion of the host range. *Pinus brutia* and *Cedrus libani* have recently been reported as host plants in Turkey (Avci 2009). Moreover, the gypsy moth at high densities attacks fruit trees e.g. apple, pear, and stone fruit trees in Germany (Mongomery & Wallner 1988; Vogt & Dickler 1993; Orozumbekov et al. 2004; Alalouni 2009; Saeidi 2011).

In North America, a wide range of tree species are hosts of the gypsy moth (Mauffette et al. 1983; Lechowicz & Mauffette 1986; Liebhold 1995). Many hypotheses have been proposed to explain the host preferences of the gypsy moth in North America e.g., phylogeny (host trees in North America should be closely related to those in Europe), plant traits, dynamics of the gypsy moth and climatic conditions (Lechowicz & Jobin 1983; Montgomery 1990; Liebhold et al. 1995). In spite of that, it was suggested that the leaf quality and the timing of eclosion relative to leaf emergence on different hosts appear more likely to determine the host preferences (Lechowicz & Mauffette 1986).

Forest susceptibility and host trees are important factors influencing the dynamics of the gypsy moth (Barbosa & Greenblatt 1979). Susceptible species provide an easily digestible and balanced diet for the gypsy moth during the different stages of the larvae (Twery 1990). Thereby, outbreaks occur more frequently on xeric sites having many susceptible host species. Such sites help to increase the insect development and to avoid natural enemies (Campbell & Solan 1977; Montgomery 1990). For example, the estimated time span between two outbreaks in xeric forests with susceptible hosts (i.e., oak and pine) is four to five years, while it is nine to ten years in mesic forests with less-susceptible hosts (i.e., mix of oak, maple, beech, birch; Johnson et al. 2006; Haynes et al. 2009; Bjornstad et al. 2010). On the other hand, the change in the chemistry and the nutritional quality of foliage during the defoliation lead to the decline of populations (Wallner & Walton 1979; Schultz & Baldwin 1982; Rossiter 1987). Additionally, spatial variations, feeding and synchrony of the egg hatch with leaf emergence of host plants are interactive factors contributing to the change of population densities (Valentine & Houston 1984; Montgomery & Wallner 1988; Leonard 1974; Hunter & Elkinton 2000).

The phenology of host plants and herbivores is mainly influenced by environmental factors. The variations in response to temperature and photoperiod determine the synchrony of

host and herbivores (Van Asch & Visser 2007). Insects also need to adapt with spatial and temporal variations to achieve synchrony with the host plants (see also Scheiner 1993; Van Dongen et al. 1997; Kawecki & Ebert 2004; Mopper 2005). Hunter (1993) suggested that the phenological synchrony has little effect on the fluctuation in the populations of the gypsy moth. The net effects of phenology on the growth of the gypsy moth population largely depend on natural-enemy effects (Hunter & Elkinton 2000). In spite of the limited evidence, the synchrony of hosts and herbivores is speculated to influence the population dynamics of univoltine insects (see Watt & Woiwod 1999; Forkner et al. 2008).

Weather

Weather, especially temperature and precipitation affect directly and indirectly the population dynamics of the gypsy moth and the synchronization of the outbreaks (Leonard 1974; Montgomery & Wallner 1988; Elkinton & Liebhold 1990; Van Asch & Visser 2007). Temperature was frequently reported to influence the hatch of egg masses, larval and pupal development and females' fecundity. Leonard (1974) reported detailed information about the influence of winter and spring temperature on the hatch time of egg masses. Winter survived eggs and the phenology of egg hatch in spring depend on temperature (Andresen et al. 2001). Temperature can also affect the population size of the gypsy moth larvae and pupae considerably e.g., high temperatures help larvae and pupae to develop faster, thereby escaping from some natural enemies (Montgomery & Wallner 1988; Leonard 1974). Precipitation reduces the ability of neonate larvae to spread and could increase spread of diseases between gypsy moth larvae (Leonard 1974). Precipitation can also be the responsible factor for the synchronization of the gypsy moth populations over large areas directly or indirectly (see Haynes et al. 2013).

Favourable weather (dry-warm) seems to support outbreaks (Delb1999). However, there is also a lack of the short and long term studies regarding the potential role of weather for the population dynamics of the gypsy moth. We speculate that much of the variability in population densities of the gypsy moth may be attributed to interacting effects of weather conditions and attack by natural enemies.

Ecological and economic impact of the gypsy moth

The ecological effects of the gypsy moth vary depending on the defoliation levels. These levels are usually related to the susceptibility of the host species, the amount of foliage removed and the number of consecutive episodes of defoliation (Muzika & Gottschalk 1995;

USDA 1995; Davidson et al. 2001). Defoliation by the gypsy moth may cause dramatic changes in tree species composition which influences also wildlife species through changes in habitat characteristics (Twery 1990; Muzika & Gottschalk 1995; Webb et al. 1995). For example, North American woodpeckers may take advantages of the habitat changes caused by defoliation of the gypsy moth (Koenig et al. 2011). Furthermore, intense defoliation can indirectly affect birds, small mammals, and even fish (Witter et al. 1992; Thurber et al. 1994; USDA 2012). One of the effects on birds is the increase in the abundance of nongame bird species due to the change in habitat characteristics (increased habitat diversity, habitat suitability and food supply; Whitmore & Greer 1991). The defoliation may also change the biological diversity as well as food web dynamics (Muzika & Gottschalk 1995). Many wildlife species depend on the host trees as a food supply. The loss of this food supply owing to tree mortality after defoliation reduces the capacity of an area to support some species, i.e., the loss of acorns for gray squirrels (Gorman & Roth 1989; Twery 1990). On the other hand, defoliation and frass decomposition can influence the soil nutrient dynamics (Hollinger 1986; Chapman et al. 2003). Recent study suggested increasing soil total C, total N and the soil NH4 pool by frass deposition. Additionally, herbivory increased soil respiration and decreased total soil N relative to ‘‘undamaged’’ controls independent of frass deposition (see Frost & Hunter 2004). However, there are inconsistent results about the influence of frass deposition on soil dynamics (see e.g. Lightfoot & Whitford 1990; Lovett & Ruesink 1995; Reynolds et al. 2000; Reynolds & Hunter 2001).

Forest trees have been categorized according to their susceptibility to defoliation. Generally, a single year of defoliation is sufficient for killing a conifer attacked by gypsy moth, while two or three successive years of defoliation are usually needed for the death of deciduous trees (Johnson & Lyon 1991). A considerable number of trees die due to the attack by other organisms after defoliation (Davidson et al. 1999; Davidson et al. 2001). The heavy attacks of *Agrilus biguttatus* (Col., Buprestidae) on oak in France was recorded after an exceptional outbreak of the gypsy moth in the previous years (Landmann 1996; Moraal & Hilszczanski 2000). In this context, different biotic and abiotic stresses may increase the susceptibility to defoliation by gypsy moths in European forests, especially in oak forests (Gottschalk & Wargo 1996; Führer 1998; Moraal & Hilszczanski 2000).

Clearly, the current management strategies have impacts on native biota (Sample et al. 1996). Products of *Bacillus thuringiensis var. kurstaki* (BTK) probably affect different species of moths more than the outbreak moth species (Schweitzer 2004). Furthermore, some chemicals, such as diflubenzuron (or Dimilin, an insect growth regulator) persist in the

environment for long time thereby affecting the forest environment and species (Sundaram et al. 1991; Lischke 1993; USDA 1995). Reports on human health and ecological assessment of the various products are also available (e.g., Forster et al. 1993; Gericke & Schellschmidt 1993; USDA 1995).

Published information on the economic impacts of the gypsy moth in its native range is limited. Some data alluding to the economic impact of the gypsy moth indirectly point to the high cost of control measures. Infested stands in Slovakia covering 18,000–22,000 ha during 1992–1994 were treated with BTK (Turcani et al. 2001b, 2003). In Germany in 1994, around 5,200 ha were treated with diflubenzuron, and around 2,000 ha were treated with BTK (Seeman 1999). The gypsy moth seems to have also considerable economic impacts on orchards. Since the 1980s, the annual defoliation of pistachio, walnut and apple orchards ranged between 17,000 and 52,000 ha in Kyrgyzstan (Orozumbekov et al. 2004). The gypsy moth caused considerable damage to poplar plantations, oak forests (1,471,839 ha), and evergreen ecosystems (3,153,882 ha) in Greece and it was controlled using chemicals and bio-insecticides (Avtzis 2001). Nevertheless, it is important to mention that no control measures have been used in some areas of Europe, e.g., in Austria since the early 1960s (Hoch et al. 2001) and in some infested stands in Germany (Seeman 1999).

In North America, more than 34 million ha have been defoliated by the gypsy moth since 1924 (McManus 2007). The estimated timber loss in 1981 in Pennsylvania alone had a value of 72 million dollars (Montgomery & Wallner 1988). Huge budgets were released to develop strategies to control this pest and to limit its spread, such as the "Slow the spread" program, one of the largest programs in the USA (Sharov et al. 2002a, b). The recently estimated costs of loss caused by the gypsy moth and other foliage feeders in the USA and the government expenditures to manage these pests range between 4 and 120 million dollars annually (see Aukema 2011).

Many studies predict an increase in the potential economic and ecological damage caused by forest pests in the future due to climate change, which may increase the likelihood of pest establishment in new locations as well as the impacts of both native and introduced pests (Logan et al. 2003; Regniere et al. 2009; FAO 2010). This prediction includes the gypsy moth. A modelling study (Vanhanen et al. 2007) indicated a shift in the distribution boundaries of the gypsy moth and the nun moth (*Lymantria monacha*) in Central Europe. In this model, the northern boundary will shift ca. 500–700 km to the north, and the southern boundary will shift ca. 100–900 km to the north. This shift threatens forests in the new areas (Vanhanen et al. 2007).

Conclusions

The damage and defoliation caused by the gypsy moth in its native range are less severe than that caused in its new ranges. This can be interpreted as a result of the release from natural enemies in the new ranges. Natural enemies are considered to be the dominant mortality factor in insect populations (Cornell et al. 1998).They could cause local extinction of native populations if these populations are vulnerable (Hochberg & Ives 1999). Pathogens, especially NPV in periods of outbreaks cause the highest mortality rates in all populations of the gypsy moth (Novotny 1989; Woods et al. 1991). Parasitoids can also cause high mortality rates. Tachinids are thereby the major parasitoids with a potential influence on the population dynamics of gypsy moth. While Tachinids contribute to the collapse of the population of the gypsy moth during outbreaks, parasitoids of other families contribute to regulating the populations at low densities. Parasitoids of the egg masses do not seem to cause sufficient mortality levels that influence the population of the insect. Predators cause considerable mortality rates, with birds and small mammals causing higher mortalities than invertebrates, at least in North America. Studies evaluating the other biotic and abiotic factors influencing the dynamics of gypsy moth are rare and especially with respect to the phenologies of host plants and the insect.

In spite of several decades of research on the ecology, population dynamics and the importance of natural enemies, we have little quantitative information to predict the population dynamics of this important forest pest species and to control its impact. More research about the interaction between environmental factors, host plants and parasitoids complex would help to understand more about the reasons of this insect eruption and the synchrony over large areas in Europe and North America.

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Natural enemies of the gypsy moth (Lepidoptera: Lymantriidae) at low population density

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Abstract

The gypsy moth *Lymantria dispar* (Linnaeus, 1758) is attacked by a species rich complex of natural enemies in its native range. Parasitoids might cause high mortality of this forest pest, thereby influencing its population dynamics. Among parasitoids, tachinid flies seem to cause the highest mortality rates of larvae and pupae. However, the importance of these parasitoids depends on the population density of the host. In a study of two years in the region of Lower Franconia (northern Bavaria, Germany), more than ten parasitoid species and four pathogens were detected during a low density phase of the gypsy moth. In spite of the low density of the host, the tachinids *Parasetigena silvestris* (Robineau-Desvoidy, 1863) and *Blepharipa pratensis* (Meigen, 1824) parasitized more than 65% of the larvae and pupae. Therefore, these two species, especially *P. silvestris*, are speculated to be among the most important parasitoids of the gypsy moth at low population densities.

Keywords: *Mortality, Parasitoids, population dynamics, tachinids*

Introduction

The gypsy moth, *Lymantria dispar* (Linnaeus 1758), is a forest pest that is attacked by a diverse assemblage of natural enemies in Central Europe (Giese & Schneider 1979; Elkinton & Liebhold 1990; Hoch et al 2001; Alalouni et al 2013). More than 150 species of parasitoids are known (109 Hymenoptera, 56 Diptera Grijpma 1989). However, the effects of parasitoids on the population density of the gypsy moth vary with respect to the gradation phase (Novotny 1989; Maier 1995; Novotny et al 1998; Turcani et al 2001; Alalouni et al 2013).

Parasetigena silvestris (Robineau-Desvoidy 1863) and *Blepharipa pratensis* (Meigen 1824), that attack the larvae and pupae, are among the important mortality factors in the native range of the gypsy moth (Maier 1990; Pemberton et al 1993; Eichhorn 1996; Berryman 1998; Zolubas et al 2001; Lee et al 2002; Sukovata & Fuester 2005; McManus & Csoka 2007; Lee & Pemberton 2010). These two species are univoltine and specific to the host insect (Montgomery & Wallner 1988). *Parasetigena silvestris* place their eggs directly on old larvae resting in the trunk flaps. In contrast, *B. pratensis* place them on the damaged foliage (Odell & Godwin 1984; Gould et al 1992). Hence, the density of the host larvae and number of host-damaged leaf clusters influence the oviposition response of these two parasitoids (Odell & Godwin 1979; 1984; Williams et al 1992). On the other hand, polyphagous tachinids such as *Exorista* sp. and *Compsilura* sp. do not show a similar response to changes in host density (McMannus & Coska 2007; Avci 2009; Camerini 2009). Parasitoids belonging to other families such as Braconidae and Ichneumonidae (Hymenoptera) show variations in parasitism rates in response to changes in host density. The percentage of the gypsy moth larvae attacked by these parasitoids increases at low or increasing population densities (Elkinton & Liebhold 1990; Schopf & Hoch 1997). However, the ultimate role of the parasitoids in the population dynamics of the gypsy moth, especially population cycles, remains a matter of debate.

In this paper, the mortality factors of the gypsy moth were investigated in Lower Franconia, Northern Bavaria during two years. The population density of the insect started to decrease since 2010. Therefore, natural enemies, especially the species composition of parasitoids, were investigated during the low density phase of the insect population.

Material and Methods:

Population density

Studies of egg masses, larval and pupal parasitism were conducted in two forest sites (Heidenfeld, Sulzheim) in Lower Franconia, Northern Bavaria for two years. Both sites are dominated by oaks (*Quercus robur, Q. petraea*, Fagaceae) and hornbeam (*Carpinus betulus*, Betulaceae). The most recent outbreaks of the gypsy moth were in 1993 and 2005.

To estimate the density of the gypsy moth, the number of egg masses per tree was surveyed for three years 2010, 2011 and 2012. The egg masses were counted from the ground till 2 m of the stem height. The critical threshold to start control is 1 egg mass/tree. Also pheromone traps were used to monitor the number of flying moths. The threshold for population control is 1200 moths/trap for every 100 hectare.

Sampling of egg masses, larvae and pupae

Egg masses were sampled in 2011 and 2012 before hatching (April, 2011 and March, 2012). Twenty six egg masses in 2011 and 20 in 2012 were collected. Egg masses were placed in Petri dishes at room temperature ~ 18-20°c and relative humidity of 60-70% till the middle of September. We counted the number of eggs and the number of hatched larvae and emerged parasitoids.

A total of 1852 larvae were sampled in the two years. The sampling was repeated three times during larval development. Due to the low number of larvae collected in the first year (399 larvae), the sampling frequency was doubled in the second year (1453 larvae). Methods for sampling included the beating method for the young larvae and burlap band method for the old larvae and pupae (old larvae will congregate under bands during the day or afternoon for shadow or hiding). The sampled larvae were placed in plastic boxes 15.5 cm × 11 cm × 6 cm in groups of ten in the lab (21°C ±1°C; 60% humidity and 16:8 L:D) and fed with fresh oak leaves (*Quercus petraea* and *Quercus robur*). Pupae were collected using the band method or directly by hand. A total of 384 pupae were sampled and placed in Petri dishes (2-3 in each plate) till the emergence of the parasitoids or the host adults. The number of parasitoids, dead larvae and pupae was counted, and the mortality caused by each factor was calculated for each year. Dead larvae with no parasitoids were moved into fridge and later sent to the Laboratory for Diagnosis, Histopathology and Electron Microscopy at Julius-Kühn Institut, Darmstadt to identify pathogens (virus, bacteria or fungi). Dead larvae which had no symptoms of parasitism or disease were recorded under “unknown mortality”.

Results

In general, the population density of the gypsy moth declined since 2010 (Table 1). The species *Anastatus* sp. (Eupelmidae) was the only parasitoid recovered from the egg masses. The percentage of egg masses in which a parasitoid was found was 42.31% in 2011 and 45% in 2012. The percentage of not hatched eggs was 3.92% (7926 eggs) and 3.59% (5438) in 2011 and 2012 respectively. Only 1.24% and 1.67% of all eggs were parasitized in each year.

Among the mortality factors detected in this study, parasitoids caused the highest mortality rates among the larvae (65.65% two years average). Unknown mortality killed 8.48% of the larvae. Pathogens caused low mortality rates (less than 5% in the two years). Most of the infected larvae showed symptoms of Nuclear Polyhydrosis Virus (mortality by NPV alone in both year was 2.81%). Nevertheless, the total mortality caused by all factors was high (78.56%, in both years for 1852 larvae; table 2).

Table 3 The density of the gypsy moth in the study sites. The number of egg masses per tree was surveyed. The egg masses were counted from the ground till 2 m of the stem height. Pheromone traps were also used to monitor the number of flying moths.

Year	Site	Moths/Trap	Egg mass/Tree
2010	Heidenfeld	2127	0.7
	Sulzheim	1765	1.5
2011	Heidenfeld	989	0.5
	Sulzheim	2429	1.5
2012	Heidenfeld	217	0.2
	Sulzheim	1104	1.0

Tachinid flies were the major mortality factor, especially on the old larvae. They caused a mortality rate up to 62.85% in two years. The mortality varied considerably between the two years. That might be attributed to the differences in the sampling sizes, and it could explain the sudden slight increase in the population density in Sulzheim. Nevertheless, *P. silvestris* caused a remarkable mortality between old larvae, especially in 2012 (71.23%). In addition to the Tachinids, *Hyposoter tricoloripes* (Viereck, 1925), *Glyptapanteles liparidis* (Bouché, 1834), and other species belong to these two families were recovered from our samples (see table 2).

Table 2 the parasitoids and diseases recovered from the larvae of the gypsy moth and the mortality rates (M). N = number of larvae attacked (parasitized or infected); M% = percentage of dead larvae to the total number of collected larvae in each year and in the two years. CL= means of confidence limits. Parenthesis represents number total number of collected larvae.

	2011		2012		Two years		
Species	**N**	**M%**	**N**	**M%**	**N**	**M%**	**CL%**
Parasetigena silvestris (Robineau-Desvoidy, 1863 Tachinidae: Diptera)	30	7.52	1035	71.23	1065	57.51	±2.3
Blepharipa pratensis (Meigen, 1824 - Diptera: Tachinidae)	14	3.51	48	3.31	62	3.33	±0.82
Compsilura concinnata (Meigen, 1824 - Diptera: Tachinidae)	9	2.25	10	0.69	19	1.03	±0.48
Exorista sp. (Meigen, 1803 - Diptera: Tachinidae)	4	1.01			4	0.22	±0.25
unidentified tachnidae			14	0.96	14	0.75	±0.42
Glyptapanteles liparidis (Bouché, 1834 - Hymenoptera: Braconidae)	12	3.01	14	0.96	26	1.40	±0.56
Cotesia melanoscela (Ratzeburg, 1844 - Hymenoptera : Braconidae)	4	1.01			4	0.22	±0.25
Hyposoter tricoloripes (Viereck, 1925 -Hymenoptera: Ichneumonidae)	12	3.01	10	0.69	22	1.19	±0.51
Virus (NPV)	4	1.01	48	3.31	52	2.81	±0.76
Bacteria			17	1.17	17	0.92	±0.46
Microsporidia			7	0.48	7	0.38	±0.32
Fungi			6	0.41	6	0.32	±0.29
Unknown mortality	37	9.27	120	8.26	157	8.48	±1.29
Total	126 (399)	31.58	1329 (1453)	91.47	1455 (1852)	78.56	±1.91

Only few species of parasitoids caused high rates of mortality for the pupae in two years (86.19%). The tachinids caused the highest mortality rates among the other species (70.58%). The two species *P. silvestris* and *B. pratensis* were the major parasitoids recovered from the pupae. The species *Lymantrichneumon disparis* (Poda, 1761) also caused considerable mortality to pupae (8.07% in two years; for more details see table 3).

Table 3 The parasitoids of the gypsy moth pupae and the mortality rates (M). N = number of not enclosed pupae; M% = percentage of dead pupae (or not enclosed) due to parasitism to the total number of collected pupae in each year and in the two years. CL%=. CL= means of confidence limits. Parenthesis represents number total number of collected pupae.

	2011		2012		Two years		
Species	**N**	**M%**	**N**	**M%**	**N**	**M%**	**CL%**
Parasetigena silvestris (Robineau-Desvoidy, 1863-Tachinidae: Diptera)	14	17.95	176	57.52	190	49.48	±5.08
Blepharipa pratensis (Meigen, 1824 - Tachinidae: Diptera)	6	7.69	56	18.30	62	16.15	±3.76
Lymantrichneumon disparis (Poda, 1761-Ichneumonidae: Hymnoptera)	5	6.41	26	8.50	31	8.07	±2.82
Other Tachinidae	4	5.13	15	4.90	19	4.95	±2.27
Unknown	5	6.41	24	7.84	29	7.55	±2.73
Total	34 (78)	43.59	297 (306)	97.06	331 (384)	86.19	±3.53

Discussion

In summary, more than ten species of parasitoids and four pathogens (Nuclear Polyhydrosis Virus, Bacteria, Microsporidia and Fungi) were recorded during the study period on eggs, larvae and pupae. The egg parasitoids and pathogens were mortality factors of minor importance. On the other hand, the tachinids *Parasetigena silvestris and Blepharipa pratensis* parasitized a considerable number of larvae and pupae. These results are in line with recent findings that the percentage of parasitized larvae of the gypsy moth increases with latitude (Fig 1; see also Alalouni 2013).

Parasitoids of the genus *Anastatus* sp. and *Ooencyrtus kuvanae* (Howard 1910) are considered to be the most common species on the egg masses of the gypsy moth in the native range as well as in the invasive range (Leonard 1974; McMannus & Coska 2007; Elkinton & Liebhold 1990). Egg parasitism, however, has probably only a marginal influence on the population dynamics of the gypsy moth in Central Europe (Alalouni 2013). One egg parasitoid, *Anastatus sp.* was recovered from our samples. Species of *Anastatus catalonicus* (Bolivar y Pieltain 1935) and *A. japonicas* (Ashmead 1904) were previously reported from Germany (Maier 1995; Bathon 1996). Overall, the rate of parasitism on the eggs was low, but the number of egg masses, in which parasitoids were found, was high. These findings correspond to previous studies (Brown et al 1983; Brown 1984; Schaefer et al 1988; Bathon 1993; Turcani et al 2001). For example, the total egg mortality during a three years study

(1991-1993) in Slovakia did not exceed ~4.8% and in Austria no egg parasitoids were recovered in two years (Hoch et al 2001).

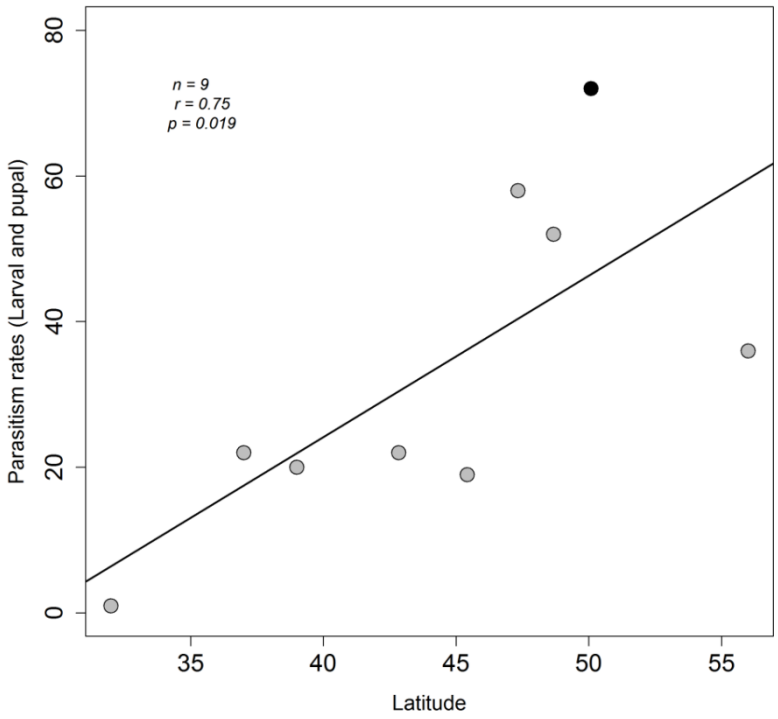

Figure 1 Relationship between latitude and percentage of parasitized larvae. For this plot, data were retrieved from various studies in Europe. The black point in the plot represents the percentage of parasitized larvae and pupae in this study. The phase of infestation, the sampling method and forests tree composition are different between the different studies, which may strongly influence this analysis. For more details see (Alalouni et al 2003)

The larval and pupal parasitoids caused the highest mortality in this study. *P. silvestris* attacked 62%of the larvae and pupae. Such high percentages of parasitized larvae by *P. silvestris* were also observed in other areas of Central Europe. In South-West Germany, 97% of the larvae were attacked by *P. silvestris* (Maier 1995; Bathon 1996). The percentage of parasitized larvae reached an average of ~48% after an outbreak in Lithuania (Zolubas et al 2001). Furthermore, *P. silvestris* is the most abundant parasitoid in Austria and Slovakia, with ~50% of larvae parasitized (Eichhorn 1996; Hoch et al 2001; Turcani et al 2001). Compared *to P. silvestris*, *Blepharipa pratensis* attacked a considerable lower percentage of larvae. The variation in the abundances of the two parasitoids seems to depend on host density with high parasitism rates during high density phases of the host (Odell & Godwin 1979; 1984; Skinner et al 1993;). Nevertheless, we found high parasitism rates at a low density population phase. Other Tachinids such as *Compsilura concinnata* (Meigen 1824) and *Exorista sp*. were rare in the samples. In contrast, these polyphagous parasitoids, especially *C. concinnata*, cause high

parasitism in invasive areas of the gypsy moth (Gould et al 1990; Skinner et al 1993; McManus & Csoka 2007).

Parasitoids from Ichneumonidae and Braconidae are common in Central Europe. Due to the biological and behavioural characteristics (i.e. life cycle, searching capability, alternative hosts), their importance as mortality factors increases during low and increasing phases densities (Fuester et al 1983; Elkinton & Liebhold 1990; Gould et al 1990; Schopf 1991; Schopf & Rembold 1993; Eichhorn 1996; Schopf & Hoch 1997; Alalouni et al 2013). Contrarily, these parasitoids were comparatively rare in the samples.

A high mortality by pathogens usually depends on high densities of larvae, non-preferred hosts, and a moist and cold climate (Weiser 1987; Murray & Elkinton 1989; Woods et al 1991). Pathogens (NPV, Bacteria, Fungi and others) killed less than 5% of the larvae. Such low mortality of entomopathogens is expected as the abundance of the gypsy moth was low during the study (Campbell & Podgwait 1971; Campbell & Sloan 1977). The "unknown mortality" even surpassed the mortality of pathogens in this study. It is a common observation in gypsy moth studies. Presently, it is not known whether this mortality is due to unknown pathogens or other factors (Campbell & Podgwaite 1971; Elkinton & Liebhold 1990; Skinner et al 1993; Turcani et al 2001).

Parasitoid-prey relationship plays an important role in the population dynamics of the gypsy moth in its native range (Berryman 1996). Maier (1995) and Hoch et al (2001) concluded that tachinid parasitoids can control the gypsy moth only in combination with other factors occurring when the density of the gypsy moth population reaches high levels. In this study, the density of the gypsy was low and decreasing. In spite of that, tachinids were main mortality factor and parasitoids of other families were unexpectedly rare. The two species *P. silvestris* and *B. prantesis* were reported to show delayed density-dependent (or second order feedback) which might explain the high frequency of them in the postgradations and declining densities of the gypsy moth (Montgomery & Wallner 1988; Turchin 1990; Berryman 1998). These results reveal the need for a better understanding of the interaction between the natural enemy assemblage and the population density of the gypsy moth in different phases. More studies that relate the percentage of attacked larvae to the density of the moth are needed.

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Summary

Sound management and conservation of insect communities and forests require a thorough understanding of the factors affecting insects and their habitats. Insects play an essential role in forest ecosystems. Many species of forest insects, e.g., the gypsy moth (*Lymantria dispar* L), impose a great danger on forests by defoliating trees. Other species, such as butterflies, are considered indicator species for nature conservation. The purpose of this dissertation is to provide some insight into the relationship between insects and forests. I use moths as a model to study the processes affecting insect assemblages, tree-insect interactions and population dynamics of insects.

In the first chapter, I present the topics of my dissertation starting with a general introduction about the roles of insects in forests. The second chapter points out the effects of environmental and neutral processes on species compositions. I particularly disentangle the effects of environmental versus spatial distance on the compositions of moth assemblages. Two statistical approaches were applied for this purpose: the raw and distance approaches. Our results show that both environmental and spatial distance influence the composition of species assemblages. Thus, environmental and neutral processes contribute to the diversity of Lepidoptera insects in Bavarian forests. However, the statistical methods (raw and distance approaches) showed inconsistent results with regard to the relative importance of each process on moth assemblages.

In the third chapter, I investigate the effects of the diversity of tree stands on insect herbivory on oak and whether the effects of tree diversity on herbivory damage are reflected by the performance (leaf consumption, growth) of the generalist herbivore *Lymantria dispar*. The study shows that the damage on oak caused by herbivores decreases with the increased diversity of tree stands. This decrease is not reflected by the performance of a generalist herbivore (*Lymantria dispar*), neither in field nor in lab assays. Hence, the changes in the tree quality do not explain the reduction of damage by herbivores. Alternative mechanisms such as natural enemies and resource dilution (associational resistance) are suggested.

In the fourth chapter, I study and review factors affecting the population dynamics of forest insects. I use the foliage feeding insect, the gypsy moth (*Lymantria dispar*), as a study-model. I highlight the role of natural enemies in the population dynamics and population cycles of the gypsy moth in its native and invasive ranges. The results show that natural enemies have a large impact on the population dynamics of the gypsy moth because they cause the highest mortality rates. Among parasitoids, the tachinids cause the highest rates of mortality in larvae and pupae populations. These mortality rates increase in the northern

latitudes. Furthermore, the effects of the parasitoids seem to be density dependent. Parasitoids are thought to influence the population cycles in the native range. In the invasive range, predators were reported to be responsible for the population cycles. Certain types of forests and host plants were additionally reported to influence population cycles in the invasive range. We speculate that the population dynamics of the gypsy moth is largely influenced by the interaction of several factors, basically weather, host plants and natural enemies. However, this may differ between native and invasive ranges.

Conclusions and outlook

This dissertation draws attention to the relationship between insects and forests. Based on my research results, I suggest the following for further work:

- First, it is of considerable importance to develop statistical methods that help to understand the patterns of the spatial variation in species compositions. The present controversies concerning the two available methods hinder further progress in our understanding.
- Second, studies on the biotic interactions between trees and insects are needed. In particular, we need more field experiments to understand the effects of tree diversity on phytophagous insects. Such experiments have to concentrate on disentangling the processes that drive relationships between host plants and insects.
- Third, studying the mortality factors of populations of forest insects is essential, because it provides us with information to understand the driving dynamics of these populations. It is particularly important to investigate factors affecting insect species with cyclic populations that cause high ecological and economic damage to forests. Without such classical studies, our predictions of insect outbreaks and the influences of climate change would be hindered.

Zusammenfassung

In Waldökosystemen haben Insekten eine sehr hohe ökologische und ökonomische Bedeutung. Viele Arten, wie z.B. der Schwammspinner (*Lymantria dispar* L.) sind bedeutende Schadinsekten, andere Lepidopteren sind durch forstwirtschaftliche Maßnahmen bedroht und gelten als Indikatorarten im Naturschutz. Ein effizientes und naturschutzfachliche fundiertes Management von Insektengemeinschaften und deren Habitate benötigt ein umfassendes Verständnis der Faktoren, welche die Verbreitung und Dynamik von Insekten in ihren natürlichen Habitaten beeinflussen. Ziel dieser Arbeit ist es, Einblicke in die Faktoren herauszuarbeiten, welche die Artenzusammensetzung und Populationsdynamik von Insekten in Waldökosystemen bedingen. Dafür werden Schmetterlinge als Modellgruppe genutzt, um räumliche Muster der Artenzusammensetzung und Populationsdynamiken sowie die beeinflussenden Umweltfaktoren zu untersuchen.

Das zweite Kapitel der Dissertation beschäftigt sich mit den Effekten von Umweltparametern und räumlicher Distanz auf Artenzusammensetzungen auf einer regionalen Skala. Hierfür wurden Daten zur Verbreitung von Schmetterlingsarten im Gebiet des Bayerns genutzt. Zwei statistische Methoden wurden zu diesem Zweck angewendet: „raw und distance approaches“. Unsere Ergebnisse zeigen, dass sowohl Umweltmerkmale, als auch räumliche Distanz die Zusammensetzung der Artengemeinschaften der Lepidopteren beeinflussen. Allerdings zeigen die statistischen Methoden (raw und distance approaches) widersprüchliche Ergebnisse in Bezug auf die relativen Effekte der einzelnen Prozesse.

Im dritten Kapitel untersuche ich den Einfluss von Baumdiversität auf den Fraßdruck von herbivoren Insekten auf Eiche, sowie auf Fraß und Wachstum eines generalistischen Herbivoren (*Lymantria dispar*). Ich zeige, dass mit zunehmender Diversität von Baumbeständen der Fraßschaden durch Herbivorie in den Baumbeständen abnimmt, konnte aber keinen Einfluss der Baumdiversität auf den Fraß und das Wachstum von *L. dispar*-Larven feststellen. Daraus schließe ich, dass die Abnahme des Fraßschadens im Freiland auf die verschiedenen Prozesse der Assoziationsresistenz zurückzuführen ist.

Im vierten Kapitel untersuche ich die Faktoren, welche die Populationsdynamik von Insekten beeinflussen. Mit dem Schwammspinner (*Lymantria dispar*) als Modell begutachte ich die Rolle der natürlichen Feinde in der Populationsdynamik der Art. Darauf folgend vergleiche ich die Rolle der natürlichen Feinde zwischen den nativen und invasiven Verbreitungsgebieten dieses bedeutenden Forstschädlings. Die Ergebnisse zeigen, dass die natürlichen Feinde einen großen Einfluss auf die Populationsdynamik des Schwammspinners

haben, und zu den höchsten Mortalitätsraten führen. Unter den Parasitoiden verursachen die tachiniden Fliegen die höchsten Mortalitätsraten an Larven und Puppen. Die Mortalität steigt mit dem Breitengrad. Dennoch scheinen die Wirkungen der Parasitoiden abhängig von Dichte des Wirts zu sein. Im Gegensatz zum nativen Verbreitungsgebiet, wo Parasitoide für die Populationszyklen verantwortlich sind, steht im invasiven Verbreitungsgebiet vor allem Prädation als Ursache dessen in Verdacht. Zusätzlich beeinflussen Waldform und Wirtspflanze die Populationszyklen im invasiven Bereich. Daher vermuten wir, dass die Populationsdynamik des Schwammspinners durch die Interaktion von mehreren Faktoren beeinflusst wird. Solche Faktoren sind z. B. Wetter, Wirtspflanzen und natürliche Feinde.

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Abgrenzung der Eigenleistung

Soweit nicht anders erwähnt, wurden alle präsentierten Studien von mir selbst geplant, durchgeführt und ausgewertet. Das abschließende Verfassen der Manuskripte erfolgte in Zusammenarbeit mit den genannten Koautoren.

Die Daten zur Untersuchung in Kapitel 2 wurden von Dr. Jörg Müller zur Verfügung gestellt. Die Daten in Kapitel 3 wurden zum Teil von Dr. Martin Schädler erhoben. Die statistische Auswertung der Daten führte ich in enger Zusammenarbeit mit Martin Schädler und Roland Brandl.